

# Discrete-Time Dynamical Systems

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In this chapter, we introduce the concept of a **discrete-time dynamical system**, which is a major mathematical object that is used in applications across a wide range of disciplines. A discrete-time dynamical system consists of an **initial value** (also called a starting value or an initial condition) and a **rule** (sometimes called a dynamic rule) that transforms the system from the present state to a state one step ahead.

For instance, the initial value “the present population is 500” and the dynamic rule “the population doubles every three years” constitute a discrete-time dynamical system. Based on these data, we calculate the **solution** of the system, which tells us how the system evolves with time.

Using calculus, we study the **updating function**, which is an algebraic expression (formula) of the dynamic rule. By studying properties of the updating function, we learn about the corresponding dynamical system. For instance, we investigate **equilibrium points**, which are the points left unchanged by the system. As well, to further investigate a dynamical system, we develop a set of algebraic rules and geometric tools (such as **cobwebbing**).

We study a number of **applications**, including unlimited and limited population growth, exponential decay, the dynamics of the consumption of coffee and alcohol, gas exchange in the lungs, and the dynamics of competing populations. In Chapter 4 we develop theoretical concepts (limits, continuity, and derivatives) that will allow us to further analyze these applications. That is why Chapter 4 will feel a bit dry (we will see fewer applications than in this chapter)—but it will be worth it.

## 3.1

### Introduction to Discrete-Time Dynamical Systems

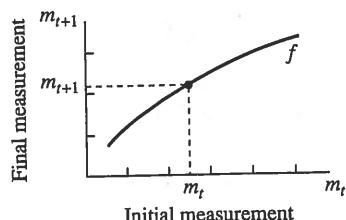
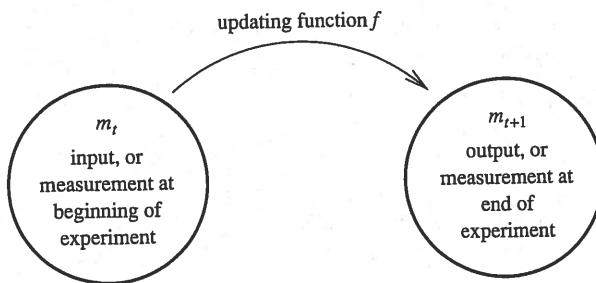
Suppose we collect data on how much several bacterial cultures grow in one hour or on how much trees grow in one year. How can we predict what will happen in the long run? In this section, we begin addressing these dynamical problems, which form the theme of this chapter and indeed a good part of this book. We follow the basic steps of applied mathematics: **quantifying the basic measurement** and describing the **dynamical rule**. We will learn how to summarize the rule with a **discrete-time dynamical system** or an **updating function** that describes change. From the discrete-time dynamical system and a starting point, called an **initial condition**, we will compute a **solution** that gives the values of the measurement as a function of time.

### Discrete-Time Dynamical Systems and Updating Functions

A discrete-time dynamical system describes the relation between a quantity measured at the beginning and the end of an experiment or a given time interval. If the measurement is represented by the variable  $m$ , we will use the notation  $m_t$  to denote the measurement at the beginning of the experiment and  $m_{t+1}$  to denote the measurement at the end of the experiment (Figure 3.1.1). Think of  $t$  as the current time and of  $t+1$  as the time one step (one unit of time) into the future. The relation between the

**FIGURE 3.1.1**

Notation for a discrete-time dynamical system

**FIGURE 3.1.2**

Updating function

initial measurement,  $m_t$ , and the final measurement,  $m_{t+1}$ , is given by the **discrete-time dynamical system**

$$m_{t+1} = f(m_t) \quad (3.1.1)$$

Note that this is the usual functional notation  $y=f(x)$ , where  $m_t$  represents the independent variable and  $m_{t+1}$  is the corresponding value of the function  $f$ . The function  $f$  is called the **updating function**. To graph  $f$ , we use a coordinate system with axes labelled  $m_t$  and  $m_{t+1}$  (see Figure 3.1.2; keep in mind that  $m_t$  is like  $x$  and  $m_{t+1}$  is like  $y$ ). Thus, the updating function  $f$  accepts the initial value (input),  $m_t$ , and returns the final value (output),  $m_{t+1}$ . Formula 3.1.1 is often referred to as a **recursion** or a **recursive relation**.

Let us consider a few examples.

### Example 3.1.1

A Discrete-Time Dynamical System for a Bacterial Population

Recall the data introduced in Example 1.3.2. Several bacterial cultures with different initial population sizes are grown in controlled conditions for one hour and then carefully measured:

Colony	Initial Population, $b_t$	Final Population, $b_{t+1}$
1	0.47	0.94
2	3.3	6.6
3	0.73	1.46
4	2.8	5.6
5	1.5	3.0
6	0.62	1.24

Note that we have replaced  $b_i$  (the initial population) with  $b_t$  (the population at time  $t$ ) and  $b_f$  (the final population) with  $b_{t+1}$  (the population at time  $t+1$ ). In this case, the number 1 in  $t+1$  represents one hour (so  $t+1$  is one hour later than  $t$ ).

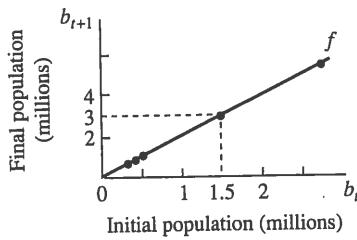
In each colony, the population doubled in size. We can describe this with the discrete-time dynamical system

$$b_{t+1} = 2b_t$$

The updating function,  $f$ , is given by

$$f(b_t) = 2b_t$$

As we have seen, the graph of the updating function plots the initial measurement,  $b_t$ , on the horizontal axis and the final measurement,  $b_{t+1}$ , on the vertical axis (Figure 3.1.3). A

**FIGURE 3.1.3**

Graph of the updating function for a bacterial population

**Example 3.1.2**

A Discrete-Time Dynamical System for Tree Growth

Suppose that we measure the height of a tree in one year and then again in the following year. Denoting the initial height by  $h_t$  and the final height by  $h_{t+1}$ , we find that

$$h_{t+1} = h_t + 0.8$$

metres. This time, the time unit 1 represents one year. The updating function is

$$f(h_t) = h_t + 0.8$$

(see Figure 3.1.4). For example, the above dynamical system predicts that a tree whose present height is  $h_t = 12.2$  m will grow to the height of

$$h_{t+1} = f(12.2) = 12.2 + 0.8 = 13 \text{ m}$$



in one year.

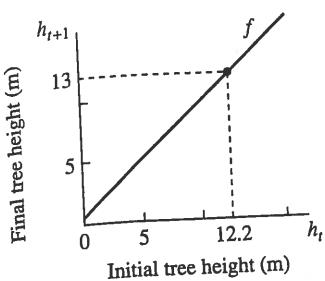


FIGURE 3.1.4

Updating function for tree growth

**Example 3.1.3**

Discrete-Time Dynamical System for Mites

Assume that a lizard in a pet store is infested by mites. The final number of mites,  $x_{t+1}$ , is related to the initial number of mites,  $x_t$ , by the formula

$$x_{t+1} = 2x_t + 30$$

where  $t$  represents time in weeks.

This formula represents the discrete-time dynamical system for the population of mites. The updating function is

$$f(x_t) = 2x_t + 30$$



The discrete-time dynamical systems for bacterial populations, tree height, and mite number were all derived from data. Often, dynamical rules can instead be derived directly from the principles governing a system.

**Example 3.1.4**

Dynamics of Absorption of Pain Medication

A patient is on methadone, a medication used to relieve chronic, severe pain (for instance after certain types of surgery). It is known that every day, the patient's body absorbs half of the methadone. In order to maintain an appropriate level of the drug, a new dosage containing 1 unit of methadone is administered at the end of each day.

By  $M_t$ , we denote the amount of methadone in the patient's body at time  $t$ . Using the language of dynamical systems, we say that  $M_t$  is the initial amount. How does the final amount,  $M_{t+1}$  (unit of time is one day), depend on  $M_t$ ?

Due to absorption,  $M_t$  is reduced to half, i.e., to  $0.5M_t$ , within a day (see Figure 3.1.5). Administering a new dosage will increase that amount by 1, and thus

$$M_{t+1} = 0.5M_t + 1$$

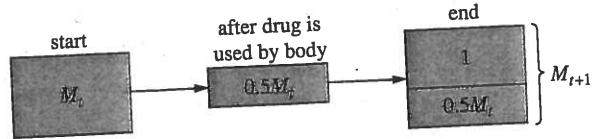


FIGURE 3.1.5

The dynamics of pain medication

So, if the patient's body contains  $M_t = 3$  units of methadone at the start of the day, the amount at the end of the day is

$$M_{t+1} = 0.5(3) + 1 = 2.5$$

If  $M_t = 1$ , then

$$M_{t+1} = 0.5(1) + 1 = 1.5$$

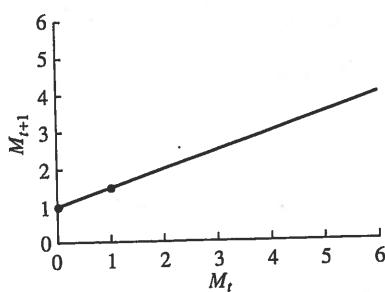


FIGURE 3.1.6

A graph of the updating function for pain medication

and so on. The updating function

$$f(M_t) = 0.5M_t + 1$$

is a line of slope 0.5 and vertical intercept 1 (Figure 3.1.6).



## Solutions

A discrete-time dynamical system describes some quantity at the end of an experiment as a function of that same quantity at the beginning. What if we were to continue the experiment? A bacterial population growing according to  $b_{t+1} = 2b_t$  would double again and again. A tree growing according to  $h_{t+1} = h_t + 0.8$  would add more and more metres to its height. An infested lizard would become even more heavily infested.

To describe a situation where a dynamical process is repeated many times, we let  $m_0$  represent the measurement at the beginning,  $m_1$  the measurement after one time step (i.e., one unit of time),  $m_2$  the measurement after two time steps, and so forth (Figure 3.1.7). In general, we define

$m_t$  = measurement  $t$  units of time after the beginning of the experiment

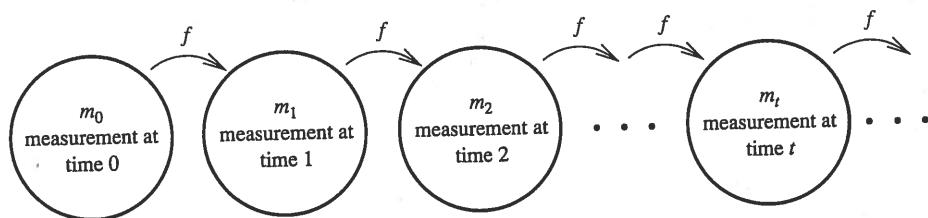


FIGURE 3.1.7

The repeated action of an updating function

Our goal is to find the values of  $m_t$  for all values of  $t$ . Before we can do so, however, we must know where we are starting. The starting value,  $m_0$ , is called the **initial condition**.

### Definition 3.1.1

The sequence of values of  $m_t$  for  $t=0, 1, 2, \dots$  is the **solution** of the discrete-time dynamical system  $m_{t+1} = f(m_t)$  starting from the **initial condition**  $m_0$ .

We say that  $m_0, m_1, m_2, m_3, \dots$  is a **recursively defined sequence**, or a **recursion**, starting from  $m_0$ .

The graph of a solution is a discrete set of points with the time,  $t$ , on the horizontal axis and the measurement,  $m_t$ , on the vertical axis. The point with coordinates  $(0, m_0)$  represents the initial condition. The point with coordinates  $(1, m_1)$  describes the measurement at  $t=1$ , and so forth (Figure 3.1.8). The point  $(100, m_{100})$  represents the measurement 100 units of time after the start of the experiment.

How do we calculate  $m_{100}$ ?

To get  $m_{100}$ , we need  $m_{99}$ , since  $m_{100} = f(m_{99})$ . To get  $m_{99}$ , we need  $m_{98}$ , and so forth. Thus, starting with  $m_0$ , we need to apply the updating function  $f$  100 times to get  $m_{100}$ . In general, to calculate  $m_t$  from  $m_0$  we need to apply  $f$  a total of  $t$  times. Is there a faster way to do this?

The answer is yes, in some simple cases, as we will witness in a moment—we will build a formula that will allow us to compute  $m_{100}$  directly from  $m_0$ , without going through all the intermediate steps. For general dynamical systems, however, such formulas are either hard to find, or they do not exist at all.

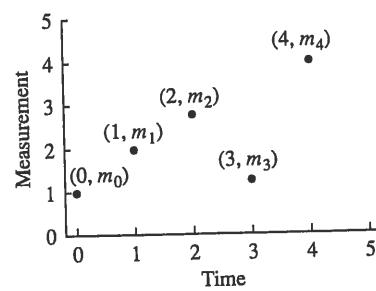


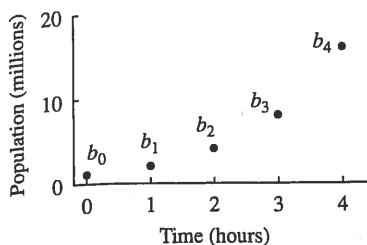
FIGURE 3.1.8

The graph of a solution

### Example 3.1.5

A Solution of the Bacterial Discrete-Time Dynamical System from Example 3.1.1

Suppose we begin with one million bacteria, which corresponds to an initial condition of  $b_0 = 1$  (with bacterial population measured in millions). If the bacteria obey the discrete-time dynamical system  $b_{t+1} = 2b_t$ , then



**FIGURE 3.1.9**  
A solution: bacterial population size as a function of time

$$\begin{aligned}b_1 &= 2b_0 = 2 \cdot 1 = 2 \\b_2 &= 2b_1 = 2 \cdot 2 = 4 \\b_3 &= 2b_2 = 2 \cdot 4 = 8\end{aligned}$$

Examining these results, we notice that

$$\begin{aligned}b_1 &= 2^1 \cdot 1 \\b_2 &= 2^2 \cdot 1 \\b_3 &= 2^3 \cdot 1\end{aligned}$$

After three hours, the population has doubled three times and is  $2^3 = 8$  times the original population. We graph the solution by plotting the time,  $t$ , on the horizontal axis and the number of bacteria after  $t$  hours ( $b_t$ ) on the vertical axis (Figure 3.1.9). The graph consists only of a discrete set of points describing the hourly measurements—hence the name *discrete-time dynamical system*. Sometimes, we will connect the points in a solution with line segments to make the pattern easier to see.

After  $t$  hours, the population will have doubled  $t$  times and will have reached the size

$$b_t = 2^t \cdot 1 \quad (3.1.2)$$

This formula describes the solution of the discrete-time dynamical system with initial condition  $b_0 = 1$ . It predicts the population after  $t$  hours of reproduction for any value of  $t$ . For example, we can compute

$$b_8 = 2^8 \cdot 1 = 256$$

without ever computing  $b_1$ ,  $b_2$ , and other intermediate values.

Now suppose that we start the system  $b_{t+1} = 2b_t$  with a different initial condition of  $b_0 = 0.3$ . We can find subsequent values by repeatedly applying the discrete-time dynamical system as follows:

$$\begin{aligned}b_1 &= 2b_0 = 2 \cdot 0.3 \\b_2 &= 2b_1 = 2(2 \cdot 0.3) = 2^2 \cdot 0.3 \\b_3 &= 2b_2 = 2(2^2 \cdot 0.3) = 2^3 \cdot 0.3\end{aligned}$$

and so on. After  $t$  hours, the population has doubled  $t$  times and reached the size

$$b_t = 2^t \cdot 0.3 \text{ million}$$

This solution is **different** from the one corresponding to the initial condition  $b_0 = 1$  (Figure 3.1.10). Although the two solutions get farther and farther apart, the ratio always remains the same (see Exercise 56). ▲

The results we obtained in Example 3.1.5 illustrate this important general model:

#### Basic Exponential Discrete-Time Dynamical System

If  $b_{t+1} = rb_t$  with initial condition  $b_0$ , then  $b_t = b_0 r^t$ .

In other words, if a population (or whatever else we are studying) changes according to

$$b_{t+1} = rb_t$$

then the population  $b_t$  at time  $t$  is equal to the initial population,  $b_0$ , multiplied by the rate,  $r$ , to the power of  $t$ .

How can we figure this out without much calculation? Assume that for the sake of argument, the time is measured in hours.

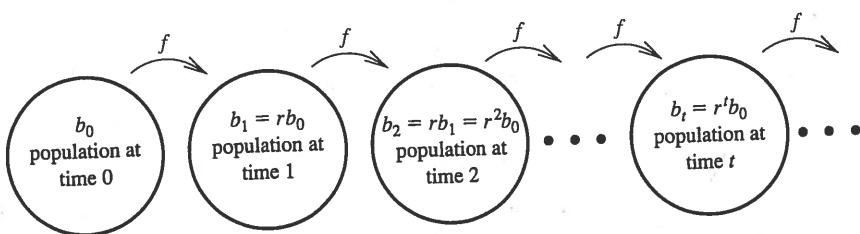


FIGURE 3.1.11

Bacterial population growth

The formula  $b_{t+1} = rb_t$  states that during each hour, the population is multiplied by the same factor,  $r$ . Thus, if the initial population is  $b_0$ , the population one hour later will be  $b_1 = rb_0$ . The population two hours later will be  $r$  times the population one hour later:

$$b_2 = rb_1 = r(rb_0) = r^2 b_0$$

Likewise,

$$b_3 = rb_2 = r(r^2 b_0) = r^3 b_0$$

and so on (see Figure 3.1.11).

### Example 3.1.6

Two Solutions of the Tree Height Discrete-Time Dynamical System

In Example 3.1.2 we studied the tree height discrete-time dynamical system

$$h_{t+1} = h_t + 0.8$$

Suppose the tree begins with a height of  $h_0 = 10$  m. Then

$$h_1 = h_0 + 0.8 = 10.8 \text{ m}$$

$$h_2 = h_1 + 0.8 = 11.6 \text{ m}$$

$$h_3 = h_2 + 0.8 = 12.4 \text{ m}$$

and so on. Each year, the height of the tree increases by 0.8 m. After three years, the height is 2.4 m greater than the original height. After  $t$  years the tree has added 0.8 m to its height  $t$  times, meaning that the height will have increased by a total of  $0.8t$  m. Therefore, the solution is

$$h_t = 10 + 0.8t \text{ m}$$

This formula predicts the height (in theory) after  $t$  years of growth for any  $t$ . We can compute, for instance,

$$h_8 = 10 + 0.8(8) = 16.4 \text{ m}$$

without computing  $h_1$ ,  $h_2$ , and other intermediate values (Figure 3.1.12).

If the tree began at the smaller size of 2 m, the size for the first few years would be

$$h_1 = h_0 + 0.8 = 2.8 \text{ m}$$

$$h_2 = h_1 + 0.8 = 3.6 \text{ m}$$

$$h_3 = h_2 + 0.8 = 4.4 \text{ m}$$

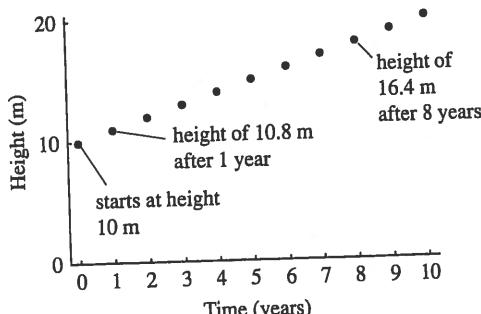


FIGURE 3.1.12

A solution: tree height as a function of time

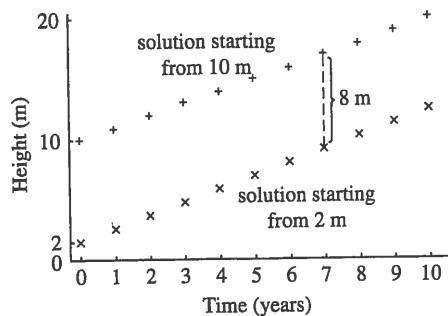


FIGURE 3.1.13

Two solutions for tree height as a function of time

and so on. Again, the tree adds  $0.8t$  m of height in  $t$  years, so the height is

$$h_t = 2 + 0.8t \text{ m}$$

The solution with this smaller initial condition is always exactly 8 m less than the solution found before (Figure 3.1.13). ▲

The solutions we obtained in Example 3.1.6 are worth remembering:

#### Basic Additive Discrete-Time Dynamical System

If  $h_{t+1} = h_t + a$  with initial condition  $h_0$ , then  $h_t = h_0 + at$ .

In the above, we assume that  $a$  is a fixed real number.

This formula is easy to verify: substituting  $t=0$  into  $h_{t+1} = h_t + a$ , we get

$$h_1 = h_0 + a$$

Similarly,

$$h_2 = h_1 + a = (h_0 + a) + a = h_0 + 2a$$

$$h_3 = h_2 + a = (h_0 + 2a) + a = h_0 + 3a$$

and so on. In other words, the solution of the dynamical system  $h_{t+1} = h_t + a$  forms an arithmetic sequence (or arithmetic progression).

We will next investigate some cases where computing the solution step by step is straightforward but finding a formula for the solution is tricky. Remarkably, there are simple discrete-time dynamical systems for which it is *impossible* to write a formula for a solution. We will meet such systems in Chapter 6.

#### Example 3.1.7

Finding a Solution of the Pain Medication Discrete-Time Dynamical System

Consider the discrete-time dynamical system for the pain medication (Example 3.1.4) given by

$$M_{t+1} = 0.5M_t + 1$$

Suppose we begin from an initial condition of  $M_0 = 5$ . Then

$$M_1 = 0.5 \cdot 5 + 1 = 3.5$$

$$M_2 = 0.5 \cdot 3.5 + 1 = 2.75$$

$$M_3 = 0.5 \cdot 2.75 + 1 = 2.375$$

$$M_4 = 0.5 \cdot 2.375 + 1 = 2.1875$$

The values are getting closer and closer to 2 (Figure 3.1.14). More careful examination indicates that the results move exactly *halfway* toward 2 each step. In particular, we find that the difference between the value of  $M_t$  and 2 is

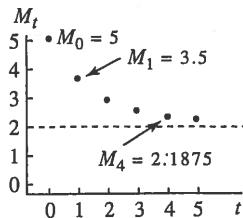


FIGURE 3.1.14

Amount of medication as a function of time

$$\begin{aligned}
 M_0 - 2 &= 5 - 2 = 3 \\
 M_1 - 2 &= 3.5 - 2 = 1.5 = 0.5 \cdot 3 \\
 M_2 - 2 &= 2.75 - 2 = 0.75 = 0.25 \cdot 3 = 0.5^2 \cdot 3 \\
 M_3 - 2 &= 2.375 - 2 = 0.375 = 0.125 \cdot 3 = 0.5^3 \cdot 3
 \end{aligned}$$

Solving for  $M_0, M_1, M_2, \dots$ , we obtain

$$\begin{aligned}
 M_0 &= 2 + 3 \\
 M_1 &= 2 + 0.5 \cdot 3 \\
 M_2 &= 2 + 0.5^2 \cdot 3 \\
 M_3 &= 2 + 0.5^3 \cdot 3
 \end{aligned}$$

and notice that

$$M_t = 2 + 0.5^t \cdot 3$$

Obviously, finding patterns in this way and translating them into formulas can be tricky. It is much more important to *describe* the behaviour of solutions with a graph or in words. In this case, our calculations suggest that the solution moves closer and closer to 2. In Section 3.2, we will develop a powerful graphical method to deduce this pattern with a minimum of calculation. ▲

The method we just used is neither intuitive nor easy to do. As well, it relies on the assumption that the numbers in the sequence  $M_1, M_2, M_3, \dots$  are getting closer and closer to 2. (Is that a sound assumption; i.e., does calculating only the numbers  $M_1$  through  $M_4$  suffice to state that the sequence  $M_1, M_2, M_3, \dots$  approaches 2? How do we know that it does not approach 2.1, or 2.05?)

We now present an alternative calculation. Assume that the solution of

$$M_{t+1} = 0.5M_t + 1$$

with initial condition  $M_0 = 5$  is of the form

$$M_t = a(0.5^t) + b$$

where  $a$  and  $b$  are real numbers whose values we now determine.

Substituting  $t = 0$ , we get

$$M_0 = a(0.5^0) + b$$

i.e.,  $5 = a + b$ . Likewise, substituting  $t = 1$  yields

$$M_1 = a(0.5^1) + b$$

and so  $3.5 = 0.5a + b$ .

In this way, we obtain a system of two equations with unknowns  $a$  and  $b$ :

$$\begin{aligned}
 a + b &= 5 \\
 0.5a + b &= 3.5
 \end{aligned}$$

Subtracting the second equation from the first, we get

$$0.5a = 1.5$$

and  $a = 3$ . From either equation we obtain that  $b = 2$ . Therefore,

$$M_t = 3 \cdot 0.5^t + 2$$

To finish, we show that  $M_t = 3 \cdot 0.5^t + 2$  indeed solves the given dynamical system. From

$$M_{t+1} = 3 \cdot 0.5^{t+1} + 2$$

and

$$0.5M_t + 1 = 0.5(3 \cdot 0.5^t + 2) + 1 = 3 \cdot 0.5^{t+1} + 1 + 1 = 3 \cdot 0.5^{t+1} + 2$$

we conclude that  $M_t$  satisfies

$$M_{t+1} = 0.5M_t + 1$$

The initial condition is satisfied as well, since

$$M_0 = 3 \cdot 0.5^0 + 2 = 5$$

### Note

The initial dose,  $M_0$ , of the medication administered is referred to as the *loading dose*. Because it is supposed to start acting as soon as possible (say, after a surgery), it is fairly high—in our case it measures five units. Subsequently, in order to keep the medication at a certain level, the patient is given a lower *maintenance dose*. In our case, the maintenance dose measures one unit.

### Example 3.1.8

A Solution of the Pain Medication Discrete-Time Dynamical System from Example 3.1.7 with Different Initial Condition

If we begin with an initial amount of  $M_0 = 1$ , then

$$M_1 = 0.5 \cdot 1 + 1 = 1.5$$

$$M_2 = 0.5 \cdot 1.5 + 1 = 1.75$$

$$M_3 = 0.5 \cdot 1.75 + 1 = 1.875$$

$$M_4 = 0.5 \cdot 1.875 + 1 = 1.9375$$

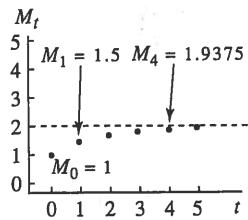


FIGURE 3.1.15

Amount of medication as a function of time

(See Figure 3.1.15.) Unlike graphs of bacterial populations (Example 3.1.5) and tree size (Example 3.1.6), the graphs of solutions starting from different initial conditions look different (compare Figures 3.1.14 and 3.1.15).

Using the technique we just introduced, we obtain the solution

$$M_t = -0.5^t + 2$$

(see also Exercise 27). □

In Section 4.2, we will use the fundamental idea of the **limit** to study more carefully what it means for the sequence of values that define a solution to get closer and closer to some number (such as 2 in Examples 3.1.7 and 3.1.8).

### Example 3.1.9

Special Solution of the Pain Medication Discrete-Time Dynamical System

Once again, we consider the system from Example 3.1.4,

$$M_{t+1} = 0.5M_t + 1$$

but this time with initial condition  $M_0 = 2$ . From

$$M_1 = 0.5M_0 + 1 = 0.5(2) + 1 = 2$$

we see that the output ( $M_1$ ) is the same as the input ( $M_0$ ). Likewise,

$$M_2 = 0.5M_1 + 1 = 0.5(2) + 1 = 2$$

$$M_3 = 0.5M_2 + 1 = 0.5(2) + 1 = 2$$

and so  $M_t = 2$  for all  $t$ .

In other words, the value  $M_0 = 2$  is not changed by the dynamical system (clearly,  $M_0 = 5$  and  $M_0 = 1$  from Examples 3.1.7 and 3.1.8 do not share this property).

Values that remain unchanged when subjected to a dynamical system are called **equilibria**. As they are important for our understanding of how the system works, we study them extensively in the following section. □

**Example 3.1.10** A Solution of the Mite Population Discrete-Time Dynamical System

Recall the discrete-time dynamical system (Example 3.1.3)

$$x_{t+1} = 2x_t + 30$$

for mites. If we start the lizard off with  $x_0 = 10$  mites, we compute

$$x_1 = 2x_0 + 30 = 50$$

$$x_2 = 2x_1 + 30 = 130$$

$$x_3 = 2x_2 + 30 = 290$$

The pattern is not at all obvious in this case. There is a pattern, however, which it is a good challenge to find (Exercise 40). ▲

## Manipulating Updating Functions

All of the operations that can be applied to ordinary functions can be applied to updating functions, but with special interpretations. We will study **composition** of an updating function with itself, find the **inverse** of an updating function, and convert the units or **translate the dimensions** of a discrete-time dynamical system.

**Composition** Consider the discrete-time dynamical system

$$m_{t+1} = f(m_t)$$

with updating function  $f$ . What does the composition  $f \circ f$  mean? The updating function **updates** the measurement by one time step. Then

$$\begin{aligned} (f \circ f)(m_t) &= f(f(m_t)) && \text{definition of composition} \\ &= f(m_{t+1}) && \text{definition of updating function} \\ &= m_{t+2} && \text{updating function applied to } m_{t+1} \end{aligned}$$

Therefore,

$$(f \circ f)(m_t) = m_{t+2}$$

The composition of an updating function with itself corresponds to a two-step updating function (Figure 3.1.16).

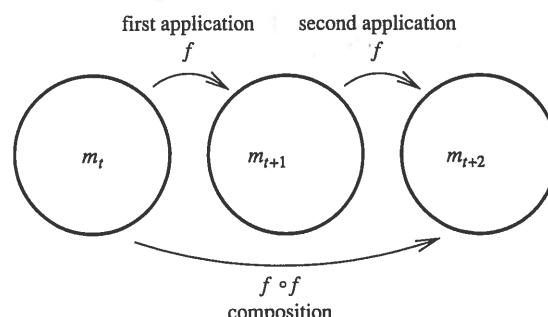


FIGURE 3.1.16

Composition of an updating function with itself

**Example 3.1.11** Composition of the Bacterial Population Updating Function with Itself

Recall that in Example 3.1.1, the bacterial updating function is  $f(b_t) = 2b_t$ . The function  $f \circ f$  takes the population size at time  $t$  as input and returns the population size two hours later, at time  $t + 2$ , as output. We can compute  $f \circ f$  with the steps

$$(f \circ f)(b_t) = f(f(b_t)) = f(2b_t) = 2(2b_t) = 4b_t$$

After two hours, the population is four times as large, having doubled twice. ▲

**Example 3.1.12** Composition of the Mite Population Updating Function with Itself

The composition of the mite population updating function  $f(x_t) = 2x_t + 30$  with itself (see Example 3.1.3) gives

$$(f \circ f)(x_t) = f(f(x_t)) = f(2x_t + 30) = 2(2x_t + 30) + 30 = 4x_t + 90$$

Suppose we started with  $x_0 = 10$  mites. After one week, we would find  $f(10) = 2 \cdot 10 + 30 = 50$  mites. After the second week, we would find  $f(50) = 2 \cdot 50 + 30 = 130$  mites. Using the composition of the updating function with itself, we can compute the number of mites after two weeks, skipping over the intermediate value of 50 mites after one week, finding

$$(f \circ f)(10) = 4 \cdot 10 + 90 = 130 \quad \blacksquare$$

Thus, composing the updating function with itself produces a function that allows us to jump two time units into the future. Beyond this obvious reason, why is this useful? Consider the following example.

**Example 3.1.13** Oscillating Dynamical System

Consider the dynamical system

$$x_{t+1} = 3.35x_t(1 - x_t)$$

with initial condition  $x_0 = 0.5$ . Using a calculator, we compute

$$x_1 = 3.35(0.5)(1 - 0.5) = 0.8375$$

$$x_2 = 3.35(0.8375)(1 - 0.8375) = 0.4559$$

$$x_3 = 3.35(0.4559)(1 - 0.4559) = 0.8310$$

$$x_4 = 3.35(0.8310)(1 - 0.8310) = 0.4705$$

and so on:  $x_5 = 0.8346$ ,  $x_6 = 0.4625$ ,  $x_7 = 0.8328$ ,  $x_8 = 0.4665$ , etc.

Starting with 0.5 and selecting every other term, we obtain the sequence

$$0.5, 0.4559, 0.4705, 0.4625, 0.4665, \dots$$

which seems to be approaching 0.46. Starting with  $x_1 = 0.8375$  and selecting every other term again, we arrive at the sequence

$$0.8375, 0.8310, 0.8346, 0.8328, \dots$$

which seems to be approaching 0.83.

We have discovered an important feature of the system: it oscillates (i.e., jumps between lower and higher values), with high values approaching a certain number, and low values approaching a certain number; see Figure 3.1.17.

In nature, a system with this property (with appropriate units) could describe seasonal lows and highs in populations of certain species (such as fish). \(\blacksquare\)

**Inverses** Consider again the general discrete-time dynamical system

$$m_{t+1} = f(m_t)$$

with updating function  $f$ . What does the inverse,  $f^{-1}$ , mean? The updating function updates the measurement by one time step, i.e., goes one time step into the future. Thus, the inverse function will go one step into the past,

$$f^{-1}(m_{t+1}) = m_t$$

So, the inverse of an updating function corresponds to an “updating” function that goes backwards in time (Figure 3.1.18).

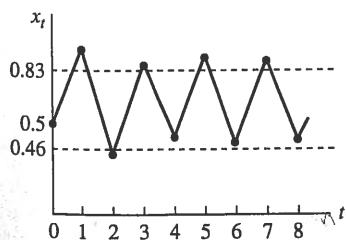


FIGURE 3.1.17

Oscillations in the dynamical system  
(vertical axis not to scale)

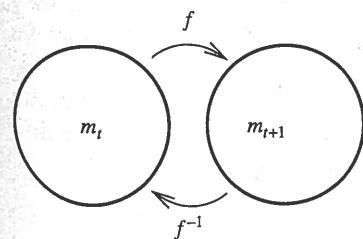


FIGURE 3.1.18

Inverse of an updating function

**Example 3.1.14** Inverse of the Bacterial Population Updating Function

The bacterial population updating function is  $f(b_t) = 2b_t$ . We find the inverse by writing the discrete-time dynamical system

$$b_{t+1} = 2b_t$$

and solving for the input variable  $b_t$ . Dividing both sides by 2 gives

$$b_t = \frac{b_{t+1}}{2}$$

The inverse function is

$$f^{-1}(b_{t+1}) = \frac{b_{t+1}}{2}$$

If multiplying by 2 describes how the population changes forward in time, dividing by 2 describes how it changes backwards in time.

For example, if  $b_t = 3$ , then

$$b_{t+1} = f(b_t) = 2b_t = 2(3) = 6$$

If we go backwards from  $b_{t+1} = 6$  using the inverse of the updating function, we find

$$b_t = f^{-1}(b_{t+1}) = f^{-1}(6) = \frac{6}{2} = 3$$

exactly where we started. 

**Example 3.1.15** Inverse of the Mite Population Updating Function

To find the inverse of the mite population updating function  $f(x_t) = 2x_t + 30$ , we solve  $x_{t+1} = 2x_t + 30$  for  $x_t$ :

$$\begin{aligned} x_{t+1} &= 2x_t + 30 \\ 2x_t &= x_{t+1} - 30 \\ x_t &= \frac{x_{t+1} - 30}{2} \\ x_t &= 0.5x_{t+1} - 15 \end{aligned}$$

Therefore,

$$x_t = f^{-1}(x_{t+1}) = 0.5x_{t+1} - 15$$

Suppose we started with  $x_t = 10$  mites. After one week, we would find

$$h(10) = 2 \cdot 10 + 30 = 50$$

mites. Applying the inverse, we find

$$h^{-1}(50) = 0.5 \cdot 50 - 15 = 10$$

mites. The inverse function takes us back to where we started. 

One reason that inverse functions are important in dynamical systems is that they allow us to go into the past. Here is an example, related to the system  $b_{t+1} = 2b_t$  that we studied in Example 3.1.14.

Assume that there are 4000 bacteria in a culture, i.e.,  $b_t = 4000$ . One hour later, the population will double, i.e.,  $b_{t+1} = 8000$ . Now, let us go back, using the inverse function

$$b_t = f^{-1}(b_{t+1}) = \frac{b_{t+1}}{2}$$

So, if  $b_{t+1} = 8000$ , then

$$b_t = \frac{b_{t+1}}{2} = \frac{8000}{2} = 4000$$

which is the number of bacteria at the beginning of the experiment. Not a big deal, we knew that already. But even before we started our experiment, the bacterial culture was growing (how did it reach its size of 4000 otherwise?). So, assuming that the dynamics of growth did not change, we can compute that one hour before our experiment started, the bacterial count was

$$b_{t-1} = \frac{b_t}{2} = \frac{4000}{2} = 2000$$

One hour before that (i.e., two hours before the start of our experiment), the bacterial count was

$$b_{t-2} = \frac{b_{t-1}}{2} = \frac{2000}{2} = 1000$$

Thus—given a dynamical system—we can run it backwards by using the inverse of the updating function in order to recover its history (if it makes sense).

## Units and Dimensions

The updating function  $f(b_t) = 2b_t$  accepts as input positive numbers with units of bacteria. If we measure this quantity in different units (say, thousands), we must convert the updating function itself into the new units. If we measure a different quantity, such as total mass or volume, we can translate the updating function into different dimensions.

### Example 3.1.16

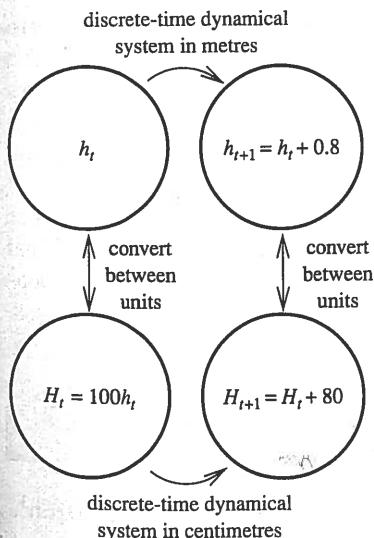


FIGURE 3.1.19

Finding the discrete-time dynamical system for trees in centimetres

### Example 3.1.17

#### Describing the Dynamics of Tree Height in Centimetres

Suppose we wish to study tree height (Example 3.1.2) in units of centimetres rather than metres. In metres, the discrete-time dynamical system is

$$h_{t+1} = f(h_t) = h_t + 0.8$$

First, we define a new variable to represent the measurement in the new units. Let  $H_t$  be tree height measured in centimetres. Then  $H_t = 100h_t$ , because there are 100 centimetres in a metre. We wish to find a discrete-time dynamical system that gives a formula for  $H_{t+1}$  in terms of  $H_t$  (Figure 3.1.19):

$$\begin{aligned} H_{t+1} &= 100h_{t+1} \\ &= 100(h_t + 0.8) \\ &= 100h_t + 80 \\ &= H_t + 80 \end{aligned}$$

The discrete-time dynamical system in the new units corresponds to adding 80 centimetres to the height, which is equivalent to adding 0.8 metres. Although the underlying process is the same, the discrete-time dynamical system and the corresponding updating function are different, just as the numerical values of measurements are different in different units. ■

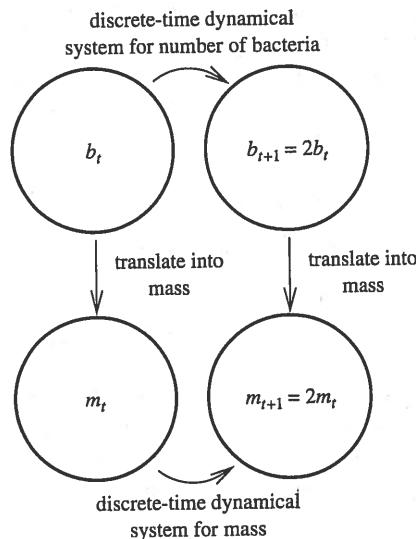
#### Describing the Dynamics of Bacterial Mass

Suppose we wish to study the bacterial population in terms of mass rather than number. Assume that  $b_{t+1} = 2b_t$  represents the dynamics of growth ( $b_t$  represents the number of bacteria at time  $t$ ). At time  $t$ , the mass, denoted by  $m_t$ , is

$$m_t = \mu b_t$$

where  $\mu$  is the mass per bacterium. The updated mass,  $m_{t+1}$ , is

$$\begin{aligned} m_{t+1} &= \mu b_{t+1} \\ &= \mu \cdot 2b_t \\ &= 2 \cdot \mu b_t \\ &= 2m_t \end{aligned}$$

**FIGURE 3.1.20**

Finding the discrete-time dynamical system for bacteria in terms of mass

This new discrete-time dynamical system doubles its input just as the original discrete-time dynamical system did, but it takes mass as its input rather than numbers of bacteria (Figure 3.1.20). ▲

**Summary**

Starting from data or an understanding of a biological process, we can derive a **discrete-time dynamical system** (also called **recursion**), the **dynamical rule** that tells how a measurement changes from one time step to the next. The **updating function** describes the relation between measurements at times  $t$  and  $t + 1$ . The **composition** of the updating function with itself produces a two-step discrete-time dynamical system, and the **inverse** of the updating function produces a backward discrete-time dynamical system. Like all biological relations, a discrete-time dynamical system can be described in different units and dimensions. Repeated application of a discrete-time dynamical system starting from an **initial condition** generates a **solution**, the value of the measurement as a function of time. With the proper combination of diligence, cleverness, and luck, it is sometimes possible to find a formula for the solution.

### 3.1 Exercises

**Mathematical Techniques**

**■ 1–4** Write the updating function associated with each discrete-time dynamical system, and evaluate it at the given arguments. Which are linear?

- $p_{t+1} = p_t - 2$ ; evaluate at  $p_t = 5$ ,  $p_t = 10$ , and  $p_t = 15$ .

- $m_{t+1} = \frac{m_t^2}{m_t + 2}$ ; evaluate at  $m_t = 0$ ,  $m_t = 8$ , and  $m_t = 20$ .

- $x_{t+1} = x_t^2 + 2$ ; evaluate at  $x_t = 0$ ,  $x_t = 2$ , and  $x_t = 4$ .

- $Q_{t+1} = \frac{1}{Q_t + 1}$ ; evaluate at  $Q_t = 0$ ,  $Q_t = 1$ , and  $Q_t = 2$ .

**■ 5–8** Compose with itself the updating function associated with each discrete-time dynamical system. Find the two-step discrete-time dynamical system. Check that the result of applying the original discrete-time dynamical system to the given initial condition twice matches the result of applying the new discrete-time dynamical system to the given initial condition once.

- Volume follows  $v_{t+1} = 1.5v_t$ , starting from  $v_0 = 1220 \mu\text{m}^3$ .

- Length obeys  $l_{t+1} = l_t - 1.7$ , starting from  $l_0 = 13.1 \text{ cm}$ .

- Population size follows  $n_{t+1} = 0.5n_t$ , starting from  $n_0 = 1200$ .

- Medication concentration obeys  $M_{t+1} = 0.75M_t + 2$ , starting from the initial condition  $M_0 = 16$ .

**■ 9–14** Find the backward discrete-time dynamical system associated with each discrete-time dynamical system. Use it to find the value at the previous time.

- $v_{t+1} = 1.5v_t$ . Find  $v_0$  if  $v_1 = 1220 \mu\text{m}^3$ .

- $l_{t+1} = l_t - 1.7$ . Find  $l_0$  if  $l_1 = 13.1 \text{ cm}$ .

- $n_{t+1} = 0.5n_t$ . Find  $n_0$  if  $n_1 = 1200$ .

- $M_{t+1} = 0.75M_t + 2$ . Find  $M_0$  if  $M_1 = 16$ .

- $p_{t+1} = \frac{4}{p_t^2}$ . Find  $p_0$  if  $p_1 = 32$ .

► 14.  $m_{t+1} = \frac{m_t}{m_t + 2}$ . Find  $m_0$  if  $m_1 = 1/5$ .

► 15–16 ■ Find the composition of each mathematically elegant updating function with itself, and find the inverse function.

15. The updating function  $f(x) = \frac{x}{1+x}$ . Remember to put things over a common denominator to simplify the composition.

16. The updating function  $h(x) = \frac{x}{x-1}$ . Remember to put things over a common denominator to simplify the composition.

► 17–20 ■ Find and graph the first five values of each discrete-time dynamical system, starting from the given initial condition. Compare the graph of the solution with the graph of the updating function.

17.  $v_{t+1} = 1.5v_t$ , starting from  $v_0 = 1220 \mu\text{m}^3$ .

18.  $l_{t+1} = l_t - 1.7$ , starting from  $l_0 = 13.1 \text{ cm}$ .

19.  $n_{t+1} = 0.5n_t$ , starting from  $n_0 = 1200$ .

20.  $M_{t+1} = 0.75M_t + 2$ , starting from the initial condition  $M_0 = 16$ .

► 21–24 ■ Using a formula for the solution, you can project far into the future without computing all the intermediate values. Find the following, and indicate whether the results are reasonable.

21. From the solution found in Exercise 17, find the volume at  $t = 20$ .

22. From the solution found in Exercise 18, find the length at  $t = 20$ .

23. From the solution found in Exercise 19, find the number at  $t = 20$ .

24. From the solution found in Exercise 20, find the concentration at  $t = 20$ .

► 25–27 ■ Find a formula for the solution of each dynamical system.

25.  $b_{t+1} = 0.8b_t - 2$ ,  $b_0 = 10$ .

26.  $x_{t+1} = 3x_t + 0.4$ ,  $x_0 = 3$ .

► 27.  $a_{t+1} = ba_t + c$ ,  $a_0 = 1$  ( $b$  and  $c$  are nonzero constants).

► 28–31 ■ Experiment with the following mathematically elegant updating functions and try to find the solution.

28. Consider the updating function

$$f(x) = \frac{x}{1+x}$$

Starting from an initial condition of  $x_0 = 1$ , compute  $x_1$ ,  $x_2$ ,  $x_3$ , and  $x_4$ , and try to spot the pattern.

29. Use the updating function in Exercise 28, but start from the initial condition  $x_0 = 2$ .

30. Consider the updating function

$$g(x) = 4 - x$$

Start from an initial condition of  $x_0 = 1$ , and try to spot the pattern. Experiment with a couple of other initial conditions. How would you describe your results in words?

31. Consider the updating function

$$h(x) = \frac{x}{x-1}$$

from Exercise 16. Start from an initial condition of  $x_0 = 3$ , and try to spot the pattern. Experiment with a couple of other initial conditions. How would you describe your results in words?

## Applications

► 32–35 ■ Consider the following actions. Which of them commute (produce the same answer when done in either order)?

32. A population doubles in size; 10 individuals are removed from a population. Try starting with 100 individuals, and then try to figure out what happens in general.

33. A population doubles in size; population size is divided by 4. Try starting with 100 individuals, and then try to figure out what happens in general.

34. An organism grows by 2 cm; an organism shrinks by 1 cm.

► 35. A person loses half her money; a person gains \$10.

► 36–39 ■ Use the formula for the solution to find the following, and indicate whether the results are reasonable.

36. Using the solution for tree height,  $h_t = 10 + 0.8t$  (Example 3.1.6), find the tree height after 20 years.

37. Using the solution for tree height,  $h_t = 10 + 0.8t$  (Example 3.1.6), find the tree height after 100 years.

38. Using the solution for bacterial population number,  $b_t = 2^t \cdot 1$  (Equation 3.1.2), find the bacterial population after 20 hours. If an individual bacterium weighs about  $10^{-12} \text{ g}$ , how much will the whole population weigh?

39. Using the solution for bacterial population number,  $b_t = 2^t \cdot 1$  (Equation 3.1.2), find the bacterial population after 40 hours.

► 40–41 ■ Try to find a formula for the solution of the given discrete-time dynamical system.

40. Find the pattern in the number of mites on a lizard, starting with  $x_0 = 10$  and following the discrete-time dynamical system  $x_{t+1} = 2x_t + 30$ . (Hint: Add 30 to the number of mites.)

41. Try to find the pattern in the number of mites on a lizard, starting with  $x_0 = 10$  and following the discrete-time dynamical system  $x_{t+1} = 2x_t + 20$ .

► 42–45 ■ The following tables display data from four experiments:

1. Cell volume after 10 minutes in a watery bath

2. Fish mass after one week in a chilly tank

3. Gnat population size after three days without food

4. Yield (in bushels) of several varieties of soybeans before and one month after fertilization

For each, graph the new value as a function of the initial value, find a simple discrete-time dynamical system, and determine the missing value in the table.

42.

Cell Volume ( $\mu\text{m}^3$ )	
Initial, $v_t$	Final, $v_{t+1}$
1220	1830
1860	2790
1080	1620
1640	2460
1540	2310
1420	??

46–49 ■ Recall the data used for Section 1.4, Exercises 60–63.

Age, $a$ (days)	Length, $L$ (cm)	Tail Length, $T$ (cm)	Mass, $M$ (g)
0.5	1.5	1.0	1.5
1	3.0	0.9	3.0
1.5	4.5	0.8	6.0
2	6.0	0.7	12.0
2.5	7.5	0.6	24.0
3	9.0	0.5	48.0

43.

Fish Mass (g)	
Initial, $m_t$	Final, $m_{t+1}$
13.1	11.4
18.2	16.5
17.3	15.6
16.0	14.3
20.5	18.8
1.5	??

44.

Gnat Population	
Initial, $n_t$	Final, $n_{t+1}$
$1.2 \cdot 10^3$	$6.0 \cdot 10^2$
$2.4 \cdot 10^3$	$1.2 \cdot 10^3$
$1.6 \cdot 10^3$	$8.0 \cdot 10^2$
$2.0 \cdot 10^3$	$1.0 \cdot 10^3$
$1.4 \cdot 10^3$	$7.0 \cdot 10^2$
$8.0 \cdot 10^2$	??

45.

Soybean Yield per Acre (bushels)	
Initial, $Y_t$	Final, $Y_{t+1}$
100	210
50	110
200	410
75	160
95	200
250	??

These data define several discrete-time dynamical systems. For example, between the first measurement (on day 0.5) and the second (on day 1), the length increases by 1.5 cm. Between the second measurement (on day 1) and the third (on day 1.5), the length again increases by 1.5 cm.

46. Graph the length at the second measurement as a function of length at the first, the length at the third measurement as a function of length at the second, and so on. Find the discrete-time dynamical system that reproduces the results.
47. Find and graph the discrete-time dynamical system for tail length.
48. Find and graph the discrete-time dynamical system for mass.
49. Find and graph the discrete-time dynamical system for age.

50–51 ■ Consider the discrete-time dynamical system  $b_{t+1} = 2b_t$  for a bacterial population (Example 3.1.1).

50. Write a discrete-time dynamical system for the total volume of bacteria (suppose each bacterium takes up  $10^4 \mu\text{m}^3$ ).
51. Write a discrete-time dynamical system for the total area taken up by the bacteria (suppose the thickness is  $20 \mu\text{m}$ ).
- 52–53 ■ Recall the equation  $r_{t+1} = r_t + 0.8$  for tree height.
52. Write a discrete-time dynamical system for the total volume of a cylindrical tree.

53. Write a discrete-time dynamical system for the total volume of a spherical tree given that  $r_{t+1} = r_t + 0.8$  (this is kind of tricky).

54–55 ■ Consider the following data describing the levels of a medication in the blood of two patients over the course of several days (measured in milligrams per litre):

Day	Medication Level in Patient 1 (mg/L)	Medication Level in Patient 2 (mg/L)
0	20	0
1	16	2
2	13	3.2
3	10.75	3.92

54. Graph three points on the updating function for the first patient. Find a linear discrete-time dynamical system for the first patient.

55. Graph three points on the updating function for the second patient, and find a linear discrete-time dynamical system.

► 56–57 ▶ For the following discrete-time dynamical systems, compute solutions starting from each of the given initial conditions. Then find the difference between the solutions as a function of time, and the ratio of the solutions as a function of time. In which cases is the difference constant, and in which cases is the ratio constant? Can you explain why?

56. Two bacterial populations follow the discrete-time dynamical system  $b_{t+1} = 2b_t$ , but the first starts with initial condition  $b_0 = 1 \times 10^6$  and the second starts with initial condition  $b_0 = 3 \times 10^5$  (in millions of bacteria).

57. Two trees follow the discrete-time dynamical system  $h_{t+1} = h_t + 0.8$ , but the first starts with initial condition  $h_0 = 10$  m and the second starts with initial condition  $h_0 = 2$  m.

► 58–61 ▶ Derive and analyze discrete-time dynamical systems that describe the following contrasting situations.

58. A population of bacteria doubles every hour, but  $1 \times 10^6$  individuals are removed after reproduction to be converted into valuable biological by-products. The population begins with  $b_0 = 3 \times 10^6$  bacteria.

- a. Find the population after one, two, and three hours.

- b. How many bacteria were harvested?

- c. Write the discrete-time dynamical system.

- d. Suppose you waited to harvest bacteria until the end of three hours. How many could you remove and still match the population  $b_3$  found in part (a)? Where did all the extra bacteria come from?

59. Suppose that a population of bacteria doubles every hour but that  $1 \times 10^6$  individuals are removed *before* reproduction to be converted into valuable biological by-products. Suppose the population begins with  $b_0 = 3 \times 10^6$  bacteria.

- a. Find the population after one, two, and three hours.

- b. Write the discrete-time dynamical system.

- c. How does the population compare with that in the previous problem? Why is it doing worse?

60. Suppose the fraction of individuals with some superior gene increases by 10% each generation.

- a. Write the discrete-time dynamical system for the fraction of organisms with the gene (denote the fraction at time  $t$  by  $f_t$  and figure out the formula for  $f_{t+1}$ ).

- b. Write the solution, starting from an initial condition of  $f_0 = 0.0001$ .

- c. Will the fraction reach 1.0? Does the discrete-time dynamical system make sense for all values of  $f_t$ ?

61. The Weber-Fechner law describes how human beings perceive differences. Suppose, for example, that a person first hears a tone with a frequency of 400 hertz (cycles per second). He is then tested with higher tones until he can hear the difference. The ratio between these values describes how well this person can hear differences.

- a. Suppose the next tone he can distinguish has a frequency of 404 hertz. What is the ratio?

- b. According to the Weber-Fechner law, the next higher tone will be greater than 404 by the same ratio. Find this tone.

- c. Write the discrete-time dynamical system for this person. Find the fifth tone he can distinguish.

- d. Suppose the experiment is repeated on a musician, and she manages to distinguish 400.5 hertz from 400 hertz. What is the fifth tone she can distinguish?

► 62–63 ▶ The total mass of a population of bacteria will change if the number of bacteria changes, if the mass per bacterium changes, or if both of these variables change. Try to derive a discrete-time dynamical system for the total mass in the following situations.

62. The number of bacteria doubles each hour, and the mass of each bacterium triples during the same time.

63. The number of bacteria doubles each hour, and the mass of each bacterium increases by  $10^{-9}$  g. What seems to go wrong with this calculation? Can you explain why?

### 3.2

### Analysis of Discrete-Time Dynamical Systems

In the previous section, we defined discrete-time dynamical systems that describe what happens during a single time step, and their solution as the sequence of values taken on over many time steps. Finding a formula for the solution is often difficult or impossible. Nonetheless, we can usually deduce the behaviour of the solution with simpler methods. This section introduces two such methods. **Cobwebbing** is a graphical technique that makes it possible to sketch solutions without calculations. Algebraically, we will learn how to solve for **equilibria**, the values for which the discrete-time dynamical system remains unchanged.

## Cobwebbing: A Graphical Solution Technique

Consider the general discrete-time dynamical system

$$m_{t+1} = f(m_t)$$

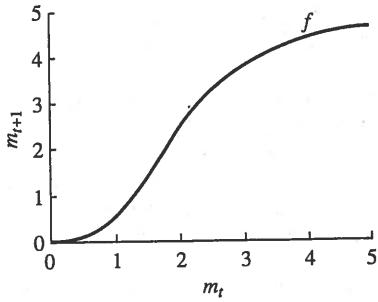
with updating function  $f$  shown in Figure 3.2.21. We now describe how, using the diagonal (i.e., the line  $m_{t+1} = m_t$ ), we can determine the behaviour of solutions graphically. The technique is called **cobwebbing**.

Suppose we are given some initial condition  $m_0$ . To find  $m_1$ , we apply the updating function

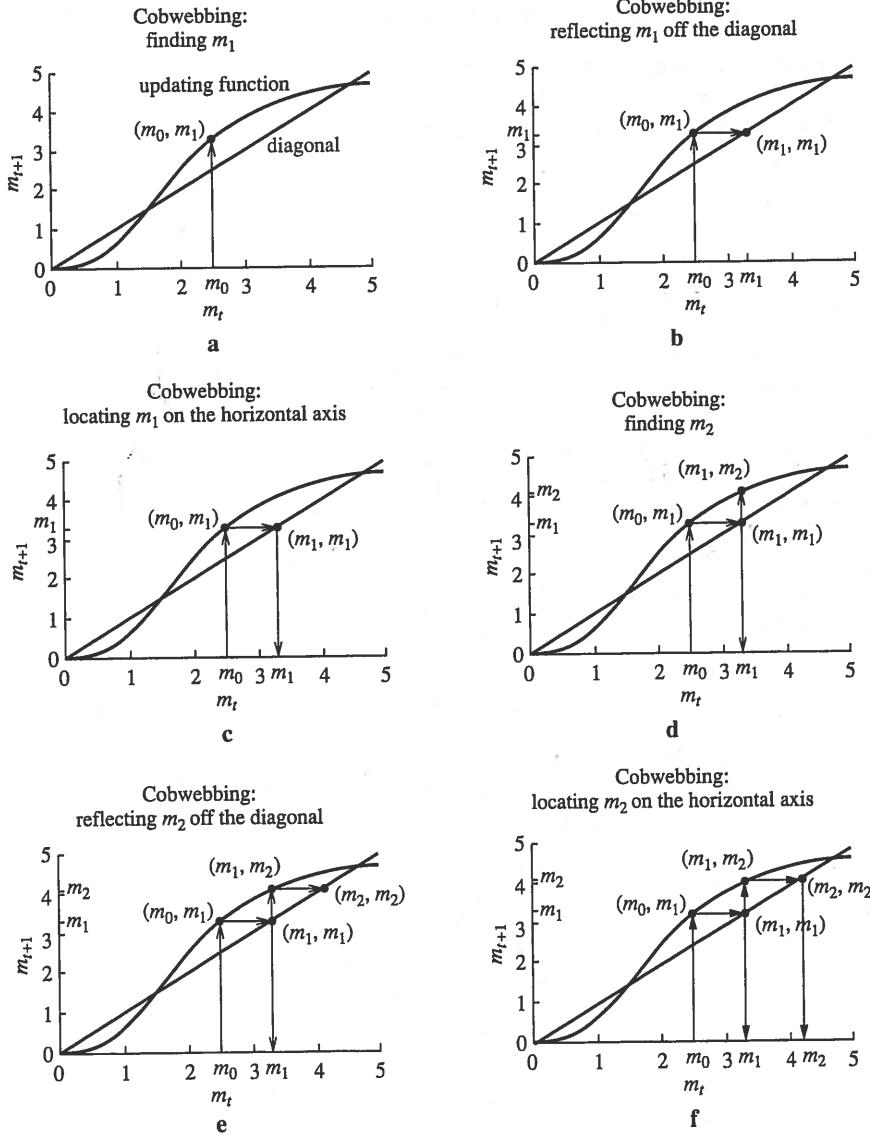
$$m_1 = f(m_0)$$

Graphically,  $m_1$  is the vertical coordinate of the point on the graph of the updating function directly above  $m_0$  (Figure 3.2.22a). Similarly,  $m_2$  is the vertical coordinate of the point on the graph of the updating function directly above  $m_1$ , and so on.

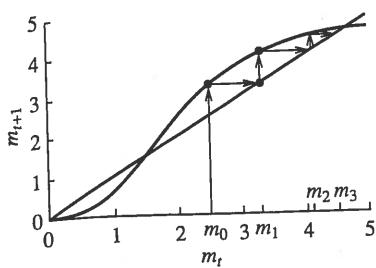
The missing step is moving  $m_1$  from the vertical axis onto the horizontal axis. The trick is to reflect it off the diagonal line that has equation  $m_{t+1} = m_t$ . Move the point  $(m_0, m_1)$  horizontally until it intersects the diagonal. Moving a point horizontally does not change the vertical coordinate, and therefore the intersection with the diagonal is the point  $(m_1, m_1)$  (Figure 3.2.22b). The point  $(m_1, 0)$  lies directly below (Figure 3.2.22c).



**FIGURE 3.2.21**  
Graph of the updating function



**FIGURE 3.2.22**  
Cobwebbing: The first steps



**FIGURE 3.2.23**  
Cobwebbing

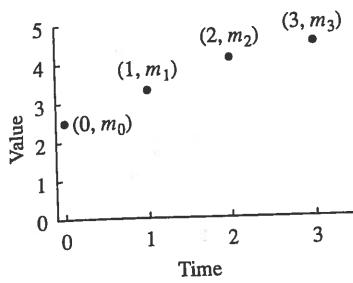
What have we done? Starting from the initial value  $m_0$ , plotted on the horizontal axis, we used the updating function to find  $m_1$  on the vertical axis and the reflecting trick to project  $m_1$  onto the horizontal axis. Now we repeat this process. Move  $m_1$  vertically to the graph of the updating function (Figure 3.2.22d), thus getting the point  $(m_1, m_2)$ . Next, we move this point horizontally until we reach the diagonal (Figure 3.2.22e), and then vertically until we reach the horizontal axis. This way, we have identified the point  $m_2$  (Figure 3.2.22f). Continuing in the same way, we obtain  $m_3, m_4$ , and so on. Because the lines reaching all the way to the horizontal axis are unnecessary, they are generally omitted to make the diagram cleaner (Figure 3.2.23).

Having found  $m_1, m_2$ , and  $m_3$  on our cobwebbing graph, we can sketch the graph of the solution that shows the measurement as a function of time. In Figure 3.2.22, we began at  $m_0 = 2.5$ . This is plotted as the point  $(0, m_0) = (0, 2.5)$  in the solution (Figure 3.2.24). The value  $m_1$  is approximately 3.2 and is plotted as the point  $(1, m_1)$  in the solution. The values of  $m_2$  and  $m_3$  increase more slowly and are shown accordingly on the graph.

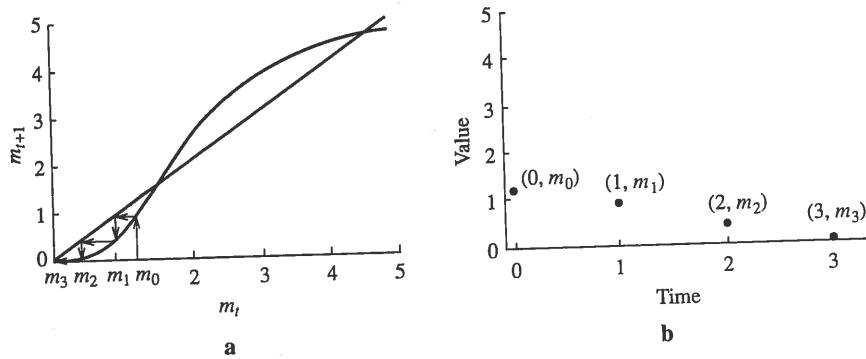
Without plugging numbers into the updating function, using the graph instead, we figured out the behaviour of a solution starting from a given initial condition.

Similarly, we can find how the given system would behave over time if we started from a different initial condition,  $m_0 = 1.2$  (Figure 3.2.25a). In this case, the diagonal lies above the graph of the updating function, so reflecting off the diagonal moves points to the left. Therefore, the solution decreases, as shown in Figure 3.2.25b.

The steps for cobwebbing are summarized in the following algorithm.



**FIGURE 3.2.24**  
The solution derived from a cobweb diagram



**FIGURE 3.2.25**  
Cobweb and solution with a different initial condition

### Algorithm 3.2.1

Using Cobwebbing to Find the Solution of  $m_{t+1} = f(m_t)$  with Initial Condition  $m_0$

1. Graph the updating function and the diagonal.
2. Starting from the initial condition on the horizontal axis, go vertically to the updating function and over to the diagonal.
3. Repeat going vertically to the updating function and over to the diagonal for as many steps as needed to find the pattern.
4. Sketch the solution at times 0, 1, 2, and so forth.

### Example 3.2.1

Cobwebbing and Solution of the Pain Medication Model

Consider the discrete-time dynamical system for the pain medication (Example 3.1.4),

$$M_{t+1} = 0.5M_t + 1$$

The updating function,  $M_{t+1} = 0.5M_t + 1$ , is a line with slope 0.5 and intercept 1, and so it is less steep than the diagonal,  $M_{t+1} = M_t$ . If we begin at  $M_0 = 5$ , the cobweb and

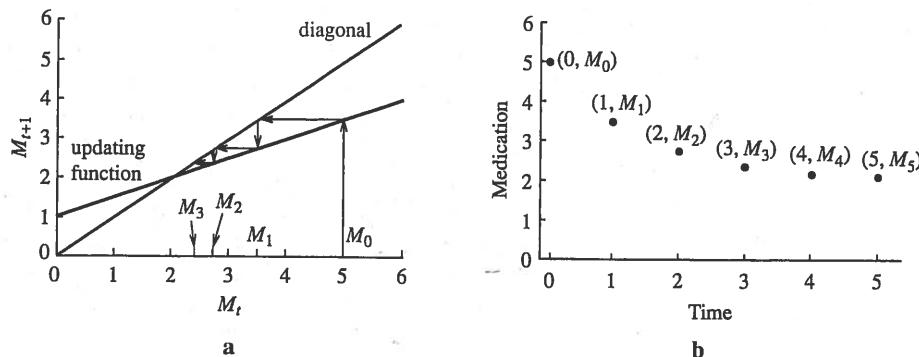


FIGURE 3.2.26

Cobweb and solution of the medication model:  $M_0 = 5$

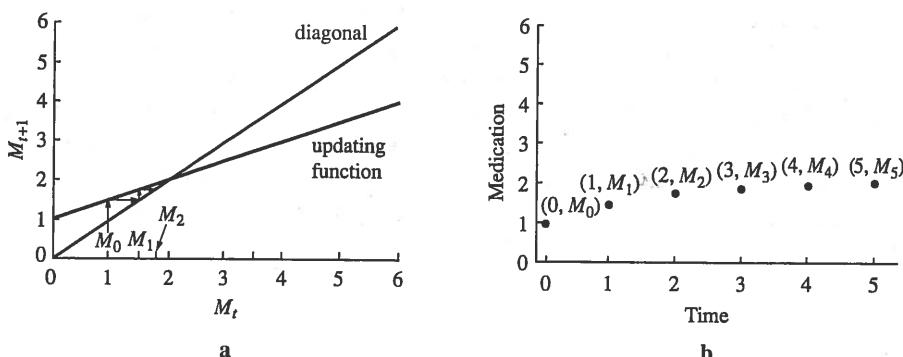


FIGURE 3.2.27

Cobweb and solution of the medication model:  $M_0 = 1$

solution decrease more and more slowly over time (Figure 3.2.26). If we begin at  $M_0 = 1$  instead, the cobweb and solution increase (at a slower and slower pace) over time (Figure 3.2.27).  $\blacktriangleleft$

## Equilibria: Geometric Approach

The points where the graph of the updating function intersects the diagonal play a special role in cobweb diagrams. These points also play an essential role in understanding the behaviour of discrete-time dynamical systems.

Consider the discrete-time dynamical systems plotted in Figure 3.2.28. The first describes a population of plants at time  $t$  (denoted by  $P_t$ ) and the second a population of birds at time  $t$  (denoted by  $B_t$ ). Each graph includes the diagonal line used in cobwebbing.

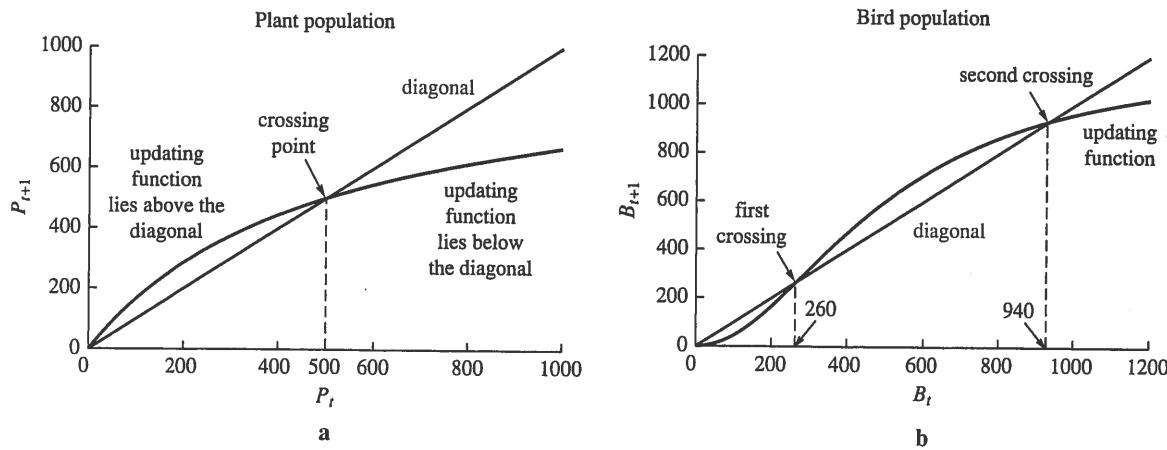
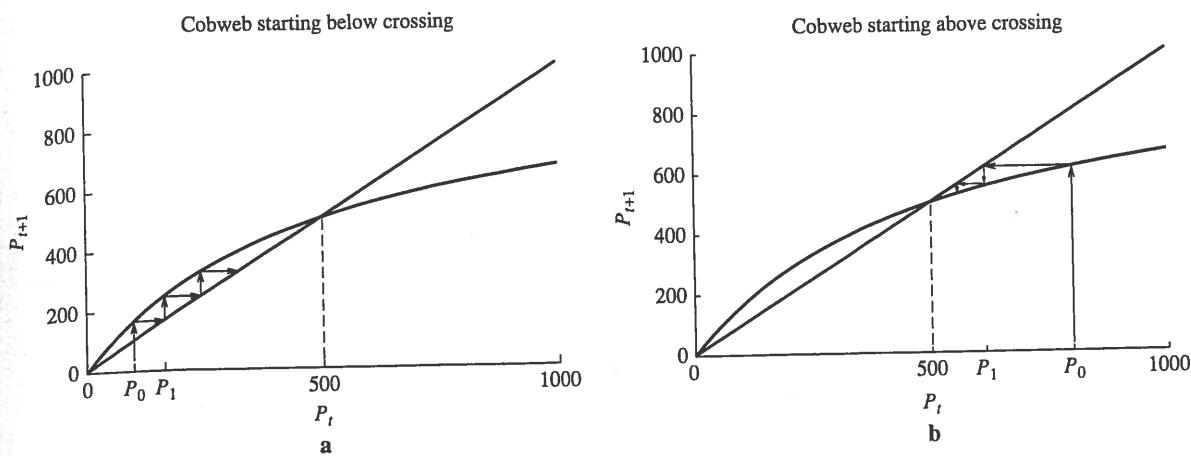


FIGURE 3.2.28

Dynamics of two populations



**FIGURE 3.2.29**  
Behaviour of plant population with two different initial conditions

If we begin cobwebbing from an initial condition where the graph of the updating function lies *above* the diagonal, the population increases (Figure 3.2.29a). In contrast, if we begin cobwebbing from an initial condition where the graph of the updating function lies *below* the diagonal, the population decreases (Figure 3.2.29b). The plant population will thus increase if the initial condition lies below the crossing point, but it will decrease if it lies above.

Similarly, the updating function for the bird population lies below the diagonal for initial conditions less than the first crossing, and the population decreases (Figure 3.2.30a). The updating function is above the diagonal for initial conditions between the crossings, and the population increases (Figure 3.2.30b). Finally, the updating function is again below the diagonal for initial conditions greater than the second crossing, and the population decreases (Figure 3.2.30c).

What happens at points where the updating function crosses the diagonal, such as  $P_0$  in Figure 3.2.31a? If we start cobwebbing from  $P_0$ , nothing much happens. The cobweb goes up to the crossing point and gets stuck there (Figure 3.2.31a). Thus, the population neither increases nor decreases, but rather remains the same (Figure 3.2.31b). The point  $P_0$  is an example of an **equilibrium point**, which we now define.

**Definition 3.2.1** A point  $m^*$  is called an equilibrium of the discrete-time dynamical system

$$m_{t+1} = f(m_t)$$

if  $f(m^*) = m^*$ .

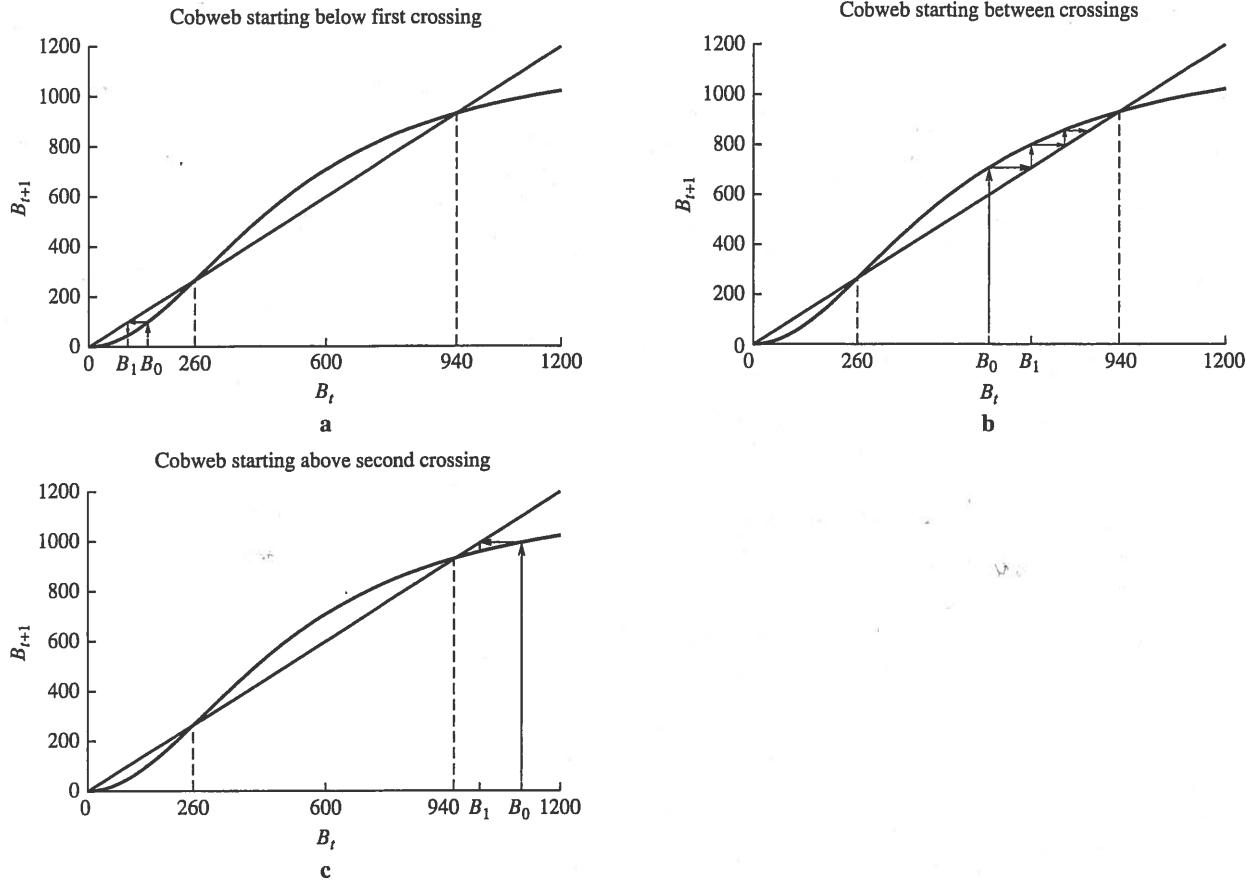
This definition says that the discrete-time dynamical system leaves  $m^*$  unchanged. These points can be found graphically by looking for intersections of the graph of the updating function with the diagonal line.

When there is more than one equilibrium, they are called **equilibria**. The plant population has two equilibria, one at  $P^* = 0$  and the other at  $P^* = 500$  (see Figure 3.2.28a). The bird population has three equilibria, located at  $B^* = 0$ ,  $B^* = 260$ , and  $B^* = 940$  (see Figure 3.2.28b).

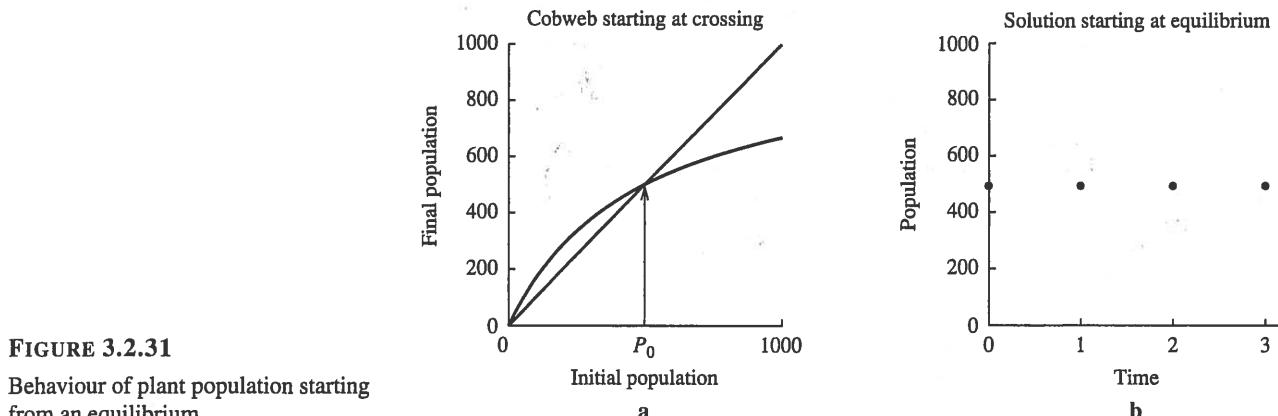
Why does the graphical method of finding equilibria work? The diagonal has the equation

$$m_{t+1} = m_t$$

and can be thought of as a discrete-time dynamical system that leaves *all* inputs unchanged, i.e., always returns an output equal to its input. The intersections of the graph of the updating function with the diagonal are the points that the updating function leaves unchanged. These are the equilibria.



**FIGURE 3.2.30**  
Behaviour of bird population starting from three different initial conditions



**FIGURE 3.2.31**  
Behaviour of plant population starting from an equilibrium

Note that the equilibria exhibit different behaviour when we cobweb starting at *nearby* points. In Figure 3.2.29a we see that the solution starting near  $P^* = 0$  moves away from it. However, the solutions that start near  $P^* = 500$  (both to the left and to the right of it) move toward the equilibrium (look at Figures 3.2.29a and 3.2.29b and imagine that the starting values  $P_0$  are closer to  $P^* = 500$ ).

### Definition 3.2.2

An equilibrium  $m^*$  is called **stable** if the solutions that start near  $m^*$  stay near or approach  $m^*$ . If the solutions that start near  $m^*$  move away from it, then  $m^*$  is an **unstable equilibrium**.

Figure 3.2.30a shows that the solution that starts at the point  $B_0$  near the equilibrium  $B^* = 0$  moves closer to it. Thus,  $B^* = 0$  is a stable equilibrium. The same figure

shows that the solution that starts near  $B^* = 260$  and to the left of it moves away from it. Figure 3.2.30b suggests that the solution starting near  $B^* = 260$  and to the right of it moves away from it. Thus,  $B^* = 260$  is an unstable equilibrium. Finally, from Figure 3.2.30b and 3.2.30c we conclude that the equilibrium  $B^* = 940$  is stable.

In Example 3.2.7 we investigate the case of a stable equilibrium for which a solution that starts near it remains there (but does not approach it). Further examples of stable and unstable equilibria appear in Section 3.4. We will discuss the concept of stability in more depth in Sections 6.7 and 6.8.

## Equilibria: Algebraic Approach

In Example 3.1.9 we discovered an input,  $M_0 = 2$ , with a special property: the given dynamical system did not change its value, i.e., the output was equal to 2 as well. In other words, the value  $M_0 = 2$  was left unchanged by the dynamical system (so it is an equilibrium point!). We now explore this phenomenon in detail.

First of all—how do we find equilibria algebraically? The answer is given in the following algorithm.

### Algorithm 3.2.2

Solving for Equilibria of the Discrete-Time Dynamical System  $m_{t+1} = f(m_t)$

1. Denoting the equilibrium point by  $m^*$ , write  $m^* = f(m^*)$ .
2. Solve the equation for  $m^*$ .
3. Think about the results. Do they make sense in the context of the given system?



### Example 3.2.2

The Equilibrium of the Pain Medication Discrete-Time Dynamical System

Recall the discrete-time dynamical system for pain medication,

$$M_{t+1} = 0.5M_t + 1$$

which we studied in Example 3.1.4. Let  $M^*$  stand for an equilibrium. The equation for equilibrium says that  $M^*$  is unchanged by the discrete-time dynamical system, or

$$M^* = 0.5M^* + 1$$

We now solve this linear equation:

$$M^* = 0.5M^* + 1$$

$$0.5M^* = 1$$

$$M^* = \frac{1}{0.5} = 2$$

The equilibrium value is 2. We can check this by plugging  $M_t = 2$  into the discrete-time dynamical system, finding that

$$M_{t+1} = 0.5 \cdot 2 + 1 = 2$$

Thus, the amount of 2 units of methadone is indeed unchanged over a course of days. Figure 3.2.32 shows that solutions that start near  $M^* = 2$  move closer to it. Thus,  $M^* = 2$  is a stable equilibrium.

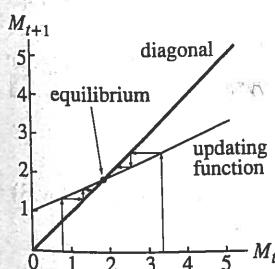


FIGURE 3.2.32

Equilibrium of the pain medication discrete-time dynamical system

### Example 3.2.3

The Equilibrium of the Bacterial Discrete-Time Dynamical System

To find the equilibria for the bacterial population discrete-time dynamical system

$$b_{t+1} = 2b_t$$

(Example 3.1.1), we write the equation for equilibria,

$$b^* = 2b^*$$

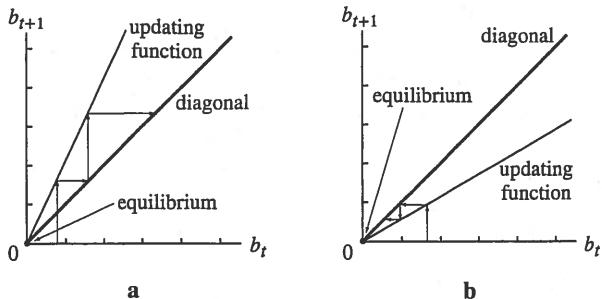


FIGURE 3.2.33

Equilibrium of the bacterial discrete-time dynamical system

from which we get  $b^* = 0$ . So there is one solution for equilibrium,  $b^* = 0$ , which makes sense: the population doubles every hour, and the only number that remains the same after doubling is zero. This conclusion is consistent with Figure 3.2.33a—the diagonal and the updating function intersect at the origin. Cobwebbing shows that the solutions that start near  $b^* = 0$  move away from it (and so  $b^* = 0$  is an unstable equilibrium). This means that even if there is a small number of bacteria to start with, the population will grow.

Now consider the dynamical system

$$b_{t+1} = 0.6b_t$$

From  $b^* = 0.6b^*$  we compute the equilibrium  $b^* = 0$ . But this time, it is a stable equilibrium, as shown using cobwebbing in Figure 3.2.33b. Thus, a population that starts with a small number of individuals will decrease in size and become extinct.  $\blacktriangle$

### Example 3.2.4

A Discrete-Time Dynamical System with No Equilibrium

The updating function for a growing tree (Example 3.1.2) following the discrete-time dynamical system

$$h_{t+1} = h_t + 0.8$$

has a graph that is parallel to the diagonal (Figure 3.2.34). To solve for the equilibria, we need to solve the equation

$$h^* = h^* + 0.8$$

Subtracting  $h^*$  from both sides, we get  $0 = 0.8$ ; i.e., the given equation has no solution. The graph of the updating function and the graph of the diagonal do not intersect because they are parallel lines. Sounds logical—something that grows 0.8 m per year cannot remain unchanged.  $\blacktriangle$

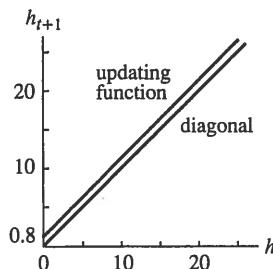


FIGURE 3.2.34

Discrete-time dynamical system for tree growth

### Example 3.2.5

Biologically Unrealistic Equilibrium

The graph of the updating function associated with a mite population (Example 3.1.3) that follows the discrete-time dynamical system

$$x_{t+1} = 2x_t + 30$$

lies above the diagonal for all values of  $x_t$  (Figure 3.2.35). To solve for the equilibria, we start with

$$x^* = 2x^* + 30$$

Solving for  $x^*$  gives  $x^* = -30$ . If we check by substituting  $x_t = -30$  into the discrete-time dynamical system, we find

$$x_{t+1} = 2 \cdot (-30) + 30 = -30$$

which is indeed equal to  $x_t$ .

Although there is a mathematical equilibrium, there is no biological equilibrium, since  $x_t$  cannot be negative. If we extend the graph to include biologically meaningless negative values, we see that the graph of the updating function does intersect the diagonal (Figure 3.2.36).

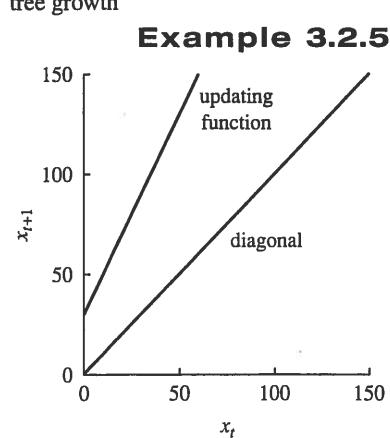


FIGURE 3.2.35

The discrete-time dynamical system for mites

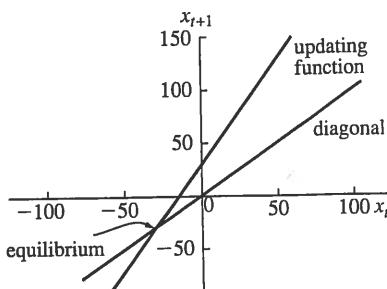


FIGURE 3.2.36

Extending the discrete-time dynamical system for mites to include a negative domain

### Example 3.2.6

Population of Codfish in Coastal Regions of Eastern Canada

Among its many objectives and activities, Canada's Atlantic Zone Monitoring Program collects data on the population of fish. The station on the eastern coast of Newfoundland monitors the Southeast Grand Banks section of the Atlantic Ocean.

The population of fish in an ocean (or lake, or river) can vary widely as it reacts to changes in the number of predators, the availability of food, the water temperature, or pollution. When all of these factors stabilize, the fish population tends to stabilize as well. A simplified model for the population of codfish in one coastal subsection of the Southeast Grand Banks is given by

$$n_{t+1} = -0.6n_t + 5.3$$

where  $n_t$  is the number of codfish in millions and  $t$  is time.

Suppose that  $n_0 = 1$ . We calculate

$$n_1 = -0.6n_0 + 5.3 = -0.6(1) + 5.3 = 4.7$$

$$n_2 = -0.6n_1 + 5.3 = -0.6(4.7) + 5.3 = 2.48$$

and, similarly,

$$n_3 = 3.81$$

$$n_4 = 3.01$$

$$n_5 = 3.49$$

$$n_6 = 3.20$$

$$n_7 = 3.38$$

and so on.

As we can see, the model does simulate fluctuations: first, they are large (from 1 million to 4.7 million, then back to 2.48 million), but, with time, they tend to get smaller and smaller, and the cod population seems to be stabilizing.

Next, we solve for the equilibrium

$$n^* = -0.6n^* + 5.3$$

$$1.6n^* = 5.3$$

$$n^* = \frac{5.3}{1.6}$$

$$n^* \approx 3.31$$

Looking at the numerical solutions, it seems that the codfish population approaches an equilibrium value of 3.31 million. To confirm our hypothesis, and to show that  $n^*$  is a stable equilibrium, we sketch the cobweb diagram (Figure 3.2.37). ▲

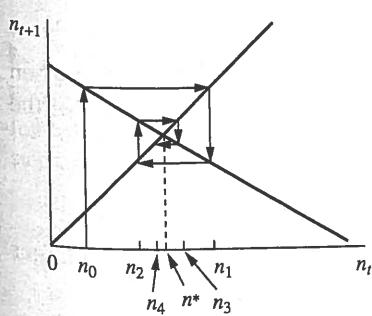


FIGURE 3.2.37

Cobwebbing codfish population

**Example 3.2.7**

A System for Which Solutions That Start Near the Equilibrium Stay Near the Equilibrium

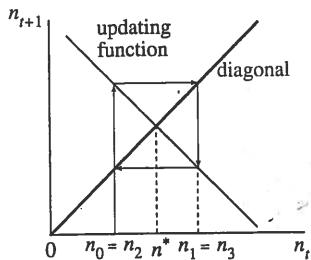


FIGURE 3.2.38

Cobwebbing the system  $n_{t+1} = -n_t + 6$

**Example 3.2.8**

Equilibria of the Pain Medication Model with a Dosage Parameter

Consider the medication discrete-time dynamical system with the parameter  $S$ ,

$$M_{t+1} = 0.5M_t + S$$

where  $S$  represents the daily dosage. Using the algorithm for finding equilibria, we get

$$M^* = 0.5M^* + S$$

$$0.5M^* = S$$

$$M^* = 2S$$

So, the equilibrium value is proportional to  $S$ , the daily dosage. Recall that in our original model (Example 3.2.2)  $S$  was equal to 1. The equilibrium was  $M^* = 2$ , which matches the above calculation.  $\blacksquare$

**Example 3.2.9**

Equilibria of the Pain Medication Model with Absorption

Consider the medication discrete-time dynamical system with parameter  $\alpha$ ,

$$M_{t+1} = (1 - \alpha)M_t + 1$$

where the parameter  $\alpha$  represents the fraction of existing medication absorbed by the body during a given day. For example, if  $\alpha = 0.1$ , 10% of the medication is absorbed by the body and 90% remains. To find the equilibrium, we solve

$$M^* = (1 - \alpha)M^* + 1$$

$$M^* - (1 - \alpha)M^* = 1$$

$$\alpha M^* = 1$$

$$M^* = \frac{1}{\alpha}$$

The equilibrium value is inversely proportional to  $\alpha$  and is therefore smaller when the fraction absorbed is larger. When  $\alpha = 0.1$ , i.e., when the body absorbs 10% of the medication each day, the equilibrium is

$$M^* = \frac{1}{0.1} = 10$$

In contrast, if the body absorbs 50% of the medication each day, leading to a larger value of  $\alpha = 0.5$ , then

$$M^* = \frac{1}{0.5} = 2$$

Thus, the body that absorbs more reaches a lower equilibrium.  $\blacksquare$

**Summary**

We have developed a graphical technique called **cobwebbing** to estimate the solutions of discrete-time dynamical systems. By examining the diagrams used for cobwebbing,

we found that intersections of the graph of the updating function with the diagonal line play a special role. These **equilibria** are points that are unchanged by the discrete-time dynamical system. Using cobwebbing, we can decide whether an equilibrium is **stable** or **unstable**. In some cases we can solve for equilibria in general, without substituting numerical values for the parameters. Solving the equations in this way can help clarify the underlying biological processes.

## 3.2 Exercises

### Mathematical Techniques

**►1-2** The following steps are used to build a cobweb diagram. Follow them for the given discrete-time dynamical systems based on bacterial populations.

- Graph the updating function.
  - Use your graph of the updating function to find the point  $(b_0, b_1)$ .
  - Reflect it off the diagonal to find the point  $(b_1, b_1)$ .
  - Use the graph of the updating function to find  $(b_1, b_2)$ .
  - Reflect off the diagonal to find the point  $(b_2, b_2)$ .
  - Use the graph of the updating function to find  $(b_2, b_3)$ .
  - Sketch the solution as a function of time.
- The discrete-time dynamical system  $b_{t+1} = 2b_t$  with  $b_0 = 1$ .
  - The discrete-time dynamical system  $n_{t+1} = 0.5n_t$  with  $n_0 = 1$ .

**►3-6** Cobweb each discrete-time dynamical system for three steps, starting from the given initial condition. Find a formula for the solution and compare your geometric answer with the algebraic answer.

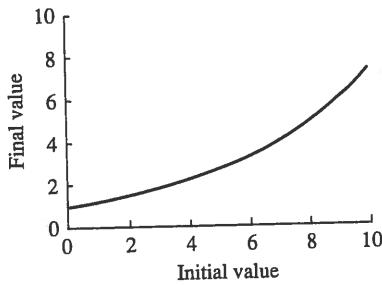
- $v_{t+1} = 1.5v_t$ , starting from  $v_0 = 1220 \mu\text{m}^3$ .
- $l_{t+1} = l_t - 1.7$ , starting from  $l_0 = 13.1 \text{ cm}$ .
- $n_{t+1} = 0.5n_t$ , starting from  $n_0 = 1200$ .
- $M_{t+1} = 0.75M_t + 2$ , starting from  $M_0 = 16 \text{ mg/L}$  (to find the algebraic solution use either the strategy employed in Example 3.1.7 or the procedure explained in the text following the example).

**►7-12** Graph the updating functions associated with the following discrete-time dynamical systems, and cobweb for four steps, starting from the given initial condition.

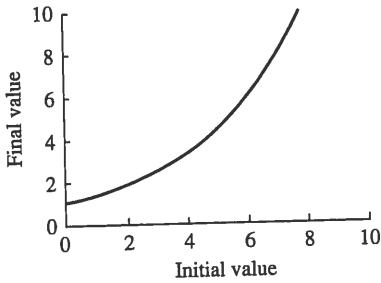
- $x_{t+1} = 2x_t - 1$ , starting from  $x_0 = 2$ .
- $z_{t+1} = 0.9z_t + 1$ , starting from  $z_0 = 3$ .
- $w_{t+1} = -0.5w_t + 3$ , starting from  $w_0 = 0$ .
- $x_{t+1} = 4 - x_t$ , starting from  $x_0 = 1$ .
- $x_{t+1} = \frac{x_t}{1+x_t}$ , starting from  $x_0 = 1$ .
- $x_{t+1} = \frac{x_t}{x_t - 1}$ , starting from  $x_0 = 3$ . Graph for  $x_t > 1$ .

**►13-16** Find the equilibria of each discrete-time dynamical system from the graph of its updating function. Label the coordinates of the equilibria. Determine whether each equilibrium is stable or unstable. If you are having difficulties cobwebbing for stability, explain why.

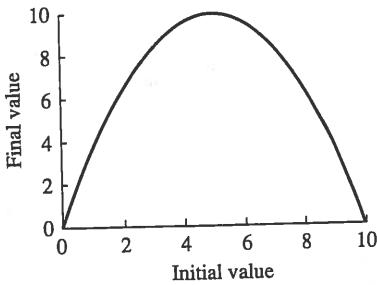
13.



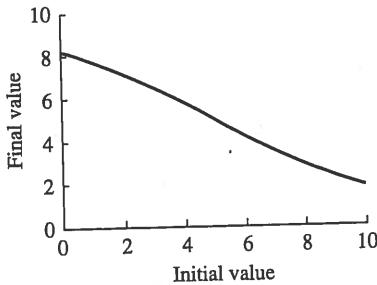
14.



15.



16.



- 17-18 ■ Sketch graphs of the following updating functions over the given range, and mark the equilibria. Find the equilibria algebraically if possible.

17.  $f(x) = x^2$  for  $0 \leq x \leq 2$   
 18.  $g(y) = y^2 - 1$  for  $0 \leq y \leq 2$

- 19-22 ■ Graph each discrete-time dynamical system. Solve for the equilibria algebraically, and identify equilibria and the regions where the updating function lies above the diagonal on your graph.

19.  $c_{t+1} = 0.5c_t + 8.0$ , for  $0 \leq c_t \leq 30$   
 20.  $b_{t+1} = 3b_t$ , for  $0 \leq b_t \leq 10$   
 21.  $b_{t+1} = 0.3b_t$ , for  $0 \leq b_t \leq 10$   
 22.  $b_{t+1} = 2b_t - 5$ , for  $0 \leq b_t \leq 10$

- 23-30 ■ Find the equilibria of each discrete-time dynamical system. Use cobwebbing to check each equilibrium for stability.

23.  $v_{t+1} = 1.5v_t$   
 24.  $l_{t+1} = l_t - 1.7$   
 25.  $x_{t+1} = 2x_t - 1$   
 26.  $z_{t+1} = 0.9z_t + 1$   
 27.  $w_{t+1} = -0.5w_t + 3$   
 28.  $x_{t+1} = 4 - x_t$ . Describe what happens when you cobweb starting at a point near the equilibrium.  
 29.  $x_{t+1} = \frac{x_t}{1+x_t}$ . Use a graphing device to obtain an accurate plot of the updating function.  
 30.  $x_{t+1} = \frac{x_t}{x_t - 1}$ . Use a graphing device to obtain an accurate plot of the updating function.

- 31-34 ■ Find the equilibria of each discrete-time dynamical system with parameter. Identify values of the parameter for which there is no equilibrium, for which the equilibrium is negative, and for which there is more than one equilibrium.

31.  $w_{t+1} = aw_t + 3$   
 32.  $x_{t+1} = b - x_t$   
 33.  $x_{t+1} = \frac{ax_t}{1+x_t}$   
 34.  $x_{t+1} = \frac{x_t}{x_t - K}$

## Applications

- 35-40 ■ Cobweb the following discrete-time dynamical system for four steps, starting from the given initial condition.

35. An alternative tree growth discrete-time dynamical system with form  $h_{t+1} = h_t + 5$  with initial condition  $h_0 = 10$ .  
 36. The mite population discrete-time dynamical system (Example 3.2.5)  $x_{t+1} = 2x_t + 30$  with initial condition  $x_0 = 0$ .  
 37. The model for the cell volume,  $v_{t+1} = 1.5v_t$ , studied in Section 3.1, Exercise 42, starting from an initial volume of 1420.

38. The model for the fish mass,  $m_{t+1} = m_t - 1.7$ , studied in Section 3.1, Exercise 43, starting from an initial mass of 13.1.  
 39. The model for the gnat population size,  $n_{t+1} = 0.5n_t$ , studied in Section 3.1, Exercise 44, starting from an initial population of 800.  
 40. The model for the yield of soybeans,  $y_{t+1} = 2y_t + 10$ , studied in Section 3.1, Exercise 45, starting from an initial yield of 20.  
 41-42 ■ Reconsider the data describing the levels of a medication in the blood of two patients over the course of several days (measured in milligrams per litre), used in Section 3.1, Exercises 54 and 55.
- | Day | Medication Level<br>in Patient 1 (mg/L) | Medication Level<br>in Patient 2 (mg/L) |
|-----|---|---|
| 0   | 20                                      | 0                                       |
| 1   | 16                                      | 2                                       |
| 2   | 13                                      | 3.2                                     |
| 3   | 10.75                                   | 3.92                                    |
41. For the first patient, graph the updating function, and cobweb starting from the initial condition on day 0. Find the equilibrium.  
 42. For the second patient, graph the updating function, and cobweb starting from the initial condition on day 0. Find the equilibrium.  
 43-44 ■ Cobweb and find the equilibrium of each discrete-time dynamical system.
43. Consider a bacterial population that doubles every hour, but  $10^6$  individuals are removed after reproduction (Section 3.1, Exercise 58). Cobweb starting from  $b_0 = 3 \times 10^6$  bacteria. Is the result consistent with the result of Exercise 58?  
 44. Consider a bacterial population that doubles every hour, but  $10^6$  individuals are removed before reproduction (Section 3.1, Exercise 59). Cobweb starting from  $b_0 = 3 \times 10^6$  bacteria. Is the result consistent with the result of Exercise 59?
- 45-46 ■ Consider the following general models for bacterial populations with harvest.
45. Consider a bacterial population that doubles every hour, but  $h$  individuals are removed after reproduction. Find the equilibrium. Does it make sense?  
 46. Consider a bacterial population that increases by a factor of  $r$  every hour, but  $1 \times 10^6$  individuals are removed after reproduction. Find the equilibrium. What values of  $r$  produce a positive equilibrium?

## Computer Exercises

47. a. Use a computer (it may have a special feature for this) to find and graph the first 10 points on the solutions of each discrete-time dynamical system. The first two describe populations with reproduction and immigration

of 100 individuals per generation, and the last two describe populations that have 100 individuals harvested or removed each generation.

- i.  $b_{t+1} = 0.5b_t + 100$ , starting from  $b_0 = 100$ .
- ii.  $b_{t+1} = 1.5b_t + 100$ , starting from  $b_0 = 100$ .
- iii.  $b_{t+1} = 1.5b_t - 100$ , starting from  $b_0 = 201$ .
- iv.  $b_{t+1} = 1.5b_t - 100$ , starting from  $b_0 = 199$ .

- b. What happens if you run the last one (part iv) for 15 steps? What is wrong with the model?

48. Compose the medication discrete-time dynamical system  $M_{t+1} = 0.5M_t + 1$  with itself 10 times. Plot the resulting function. Use this composition to find the amount of medication after 10 days, starting from amounts of 1, 5, and 18 units. If the goal is to reach a stable concentration of 2 units, do you think this is a good therapy?

### 3.3

## Modelling with Discrete-Time Dynamical Systems

In this section we investigate several discrete-time dynamical systems that describe the **consumption of drugs** (caffeine and alcohol) and model a variety of ways a **population** can change (unlimited growth, limited growth, decline in growth).

The common theme is the **per capita production**, which arises in various forms (e.g., constant functions, nonlinear functions). Algebraically, some models are fairly straightforward (consumption of caffeine, for instance), and some (alcohol consumption or limited population growth) are more involved. Although the models we discuss here do not attempt to capture all of the complexities of the situations they investigate, nevertheless they provide us with good and useful insights.

### Absorption of Caffeine

Evidence suggests that, on average, our body eliminates caffeine at a constant rate of about 13% per hour. That means that one hour after quickly finishing a small Second Cup coffee (assuming our body was clean of caffeine before that, so that now it contains about 240 mg of caffeine), the amount of caffeine present in our body will be

$$240 \text{ mg} - 0.13(240 \text{ mg}) = 208.80 \text{ mg}$$

Of course, we could have said that 87% of the caffeine is still present in our body and calculated the amount as  $0.87(240 \text{ mg}) = 208.80 \text{ mg}$ .

Let us build the model for the elimination and consumption of caffeine.

By  $c_t$  we denote the amount (in milligrams) of caffeine at time  $t$  (in hours). We need to find a formula for  $c_{t+1}$ , i.e., for the amount of caffeine one hour later. Due to elimination, the original amount of caffeine will decrease by 13%, i.e., will fall to

$$c_t - 0.13c_t = 0.87c_t$$

Assuming that at the end of the same time interval we consume  $d$  extra milligrams of caffeine, we get that

$$c_{t+1} = 0.87c_t + d$$

where  $d \geq 0$ . This dynamical system is an example of a substance absorption (elimination) and replacement (consumption) model. Of course, when  $d=0$ , there is no replacement as no new caffeine is introduced into the body.

#### Example 3.3.1

Dynamics of Caffeine Absorption: Calculations

If we have two double espressos (at 200 mg of caffeine each) and a Red Bull (80 mg of caffeine) at 10 P.M., will we be able to fall asleep by midnight?

We consider the caffeine absorption and replacement dynamical system

$$c_{t+1} = 0.87c_t + d$$

where  $c_0 = 200 \text{ mg} + 200 \text{ mg} + 80 \text{ mg} = 480 \text{ mg}$ . Since there is no replacement (we assume that after the two espressos and the Red Bull we ingest no more caffeine), we

set  $d = 0$ . Note that the initial condition assumes that there was no caffeine present in our body before we consumed the caffeine described here.

The solution of

$$c_{t+1} = 0.87c_t$$

with initial condition  $c_0 = 480$  mg is given by

$$c_t = 0.87^t \cdot 480$$

where  $t$  is time in hours measured from 10 P.M. We conclude that the amount of caffeine still present in our body at midnight will be

$$c_2 = 0.87^2 \cdot 480 \text{ mg} \approx 363.31 \text{ mg}$$

So there is still a fairly significant amount of caffeine left in our body.

How do we answer our question? Can we fall asleep with 363.31 mg of caffeine circulating through our body?

It is known that the same level of caffeine affects people in significantly different ways, so it is not possible to define a threshold, that is, to specify the amount of caffeine that, if reached or exceeded, would prevent one from falling asleep.

Let us try to provide a better answer. First, we calculate the half-life of caffeine. From

$$c_t = 0.87^t \cdot 480$$

we get

$$240 = 0.87^t \cdot 480$$

$$0.87^t = 0.5$$

$$\ln 0.87^t = \ln 0.5$$

$$t \ln 0.87 = \ln 0.5$$

$$t = \frac{\ln 0.5}{\ln 0.87}$$

$$t \approx 4.98$$

So the half-life of caffeine is about 5 h.

Reading advice on healthy sleeping from various sources, we find suggestions that it is a good idea to stop drinking coffee (ingesting caffeine) at around 2 P.M. What is a possible rationale behind this?

We just calculated that every 5 h the amount of caffeine in our body halves. So, after two half-life intervals—which end at midnight, the time we might want to go to bed—a quarter of the original amount of caffeine will be present. Thus, even a relatively high amount of caffeine taken by 2 P.M. will decay to a relatively small amount by midnight.

According to Health Canada guidelines, the recommended maximum daily caffeine intake for healthy adults is 400 mg. So if we have those two double espressos and the Red Bull at 10 P.M., the amount of caffeine present at midnight (363.31 mg) is quite close to the suggested maximum daily intake. So, the best answer to our question is—do not do it!

## Elementary Population Models

In previous sections we studied the case where the bacterial population doubles every hour—that is, each bacterium divides once and both daughter bacteria survive.

In a more realistic scenario, we assume that only a fraction of the daughters survive. For example, if each offspring has a 75% chance of survival, then there will be,

on average, 1.5 surviving offspring per parent. In this case, the dynamical system for the bacteria population can be written as

$$b_{t+1} = 1.5b_t$$

Likewise, the system

$$b_{t+1} = 1.2b_t$$

describes the situation where each of the two daughters has a 60% chance of survival, and thus each parent produces, on average, 1.2 bacteria.

Motivated by this, we consider the general system

$$b_{t+1} = rb_t$$

where  $r$  represents the number of new bacteria produced *per bacterium*. The constant  $r$  is called the **per capita production**.

This important equation of population biology states that the population at time  $t+1$  is equal to the per capita production (the number of new bacteria per old bacterium) multiplied by the population at time  $t$ , or

$$\text{new population} = \text{per capita production} \times \text{old population}$$

Recall that the solution of  $b_{t+1} = rb_t$  is given by

$$\text{population at time } t = \text{initial population} \times \text{rate } r \text{ to the power of } t$$

i.e.,  $b_t = b_0 r^t$ , where  $b_0$  is the initial condition.

### Example 3.3.2 Discrete-Time Dynamical System for Bacteria

Recall that we studied the case

$$b_{t+1} = 2b_t$$

in detail in Example 3.1.5. This is the case where each daughter survives with the chance of  $r/2 = 2/2 = 100\%$ , i.e., each parent is replaced by two daughters, and so the population doubles each hour. For example, if  $b_0 = 1000$ , then  $b_1 = 2000$  (Figure 3.3.39a).

Consider the case where  $r = 1.5$  (recall that this means that each of the two offspring has an  $r/2 = 1.5/2 = 75\%$  chance of survival, or, put differently, three of four offspring will survive). The discrete-time system is

$$b_{t+1} = 1.5b_t$$

If  $b_0 = 1000$ , then  $b_1 = 1500$ , so the population increases by 50% (Figure 3.3.39b) in each generation.

The case when  $r = 1$ ,

$$b_{t+1} = b_t$$

describes the population in which each daughter survives with a chance of  $r/2 = 1/2 = 50\%$ ; stated differently, one in two offspring will survive. This means that the surviving offspring replaces the parent, and thus there is no change in the numbers. Indeed, if  $b_0 = 1000$ , then  $b_1 = 1000$  as well (Figure 3.3.39c).

The system

$$b_{t+1} = 0.5b_t$$

represents a population with high mortality: the chance of a daughter surviving is  $r/2 = 0.5/2 = 25\%$ ; i.e., one in four offspring will survive. In this case, starting with  $b_0 = 1000$  bacteria, the population will fall to  $b_1 = 500$  bacteria in one hour. Thus, every hour, the population decreases by 50% (Figure 3.3.39d).

Numerical values for the four different dynamics (all with the same initial condition) are given in Table 3.3.1.

In the first two columns,  $r > 1$  and the population increases every hour (at different rates). When  $r = 1$ , the population remains the same hour after hour. In the final

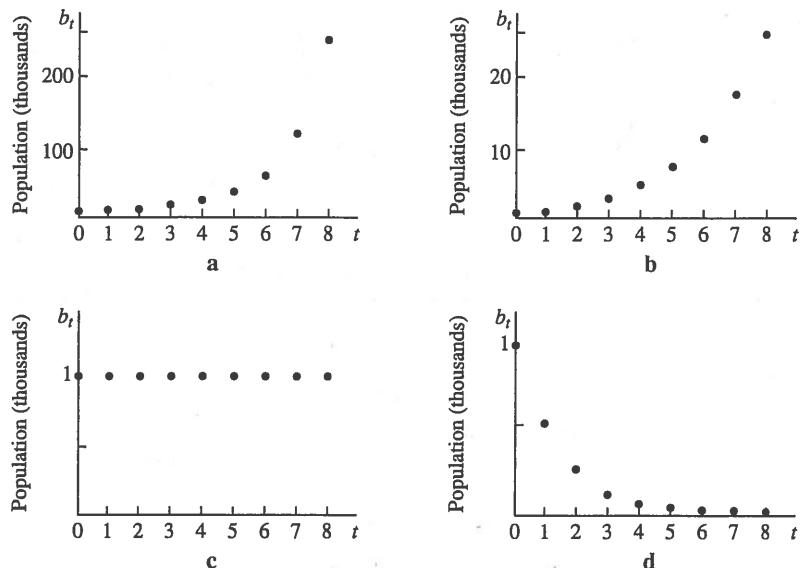


FIGURE 3.3.39

Growing, unchanged, and declining bacterial populations

Table 3.3.1

$t$	Population (in Thousands)			
	$r=2$	$r=1.5$	$r=1$	$r=0.5$
0	1	1	1	1
1	2	1.5	1	0.5
2	4	2.25	1	0.25
3	8	3.375	1	0.125
4	16	5.0625	1	0.0625
5	32	7.59375	1	0.03125
6	64	11.39063	1	0.01563
7	128	17.08594	1	0.00781
8	256	25.62891	1	0.00391

Table 3.3.2

Value of $r$	Behaviour of Population
$r > 1$	population increases
$r = 1$	population remains constant
$r < 1$	population decreases

column, when  $r < 1$ , the population decreases. We summarize these observations in Table 3.3.2.

Our model,  $b_{t+1} = rb_t$ , assumes that the per capita production is constant; i.e., it assumes that each bacterium produces  $r$  new bacteria (on average) *no matter what the total population is* (as shown in Figure 3.3.40).

Consider the case  $r = 1.5$ . Regardless of the current population of bacteria ( $b_t$  could be 100, or 5000, or 1,000,000), each bacterium will produce, on average, 1.5 offspring. Is this realistic?

Resources (space, food) are always limited, and, as the number of bacteria grows, so does competition for resources. This will, in turn, force the population to reduce its production of offspring. So if we wish to build a model for the population that reflects

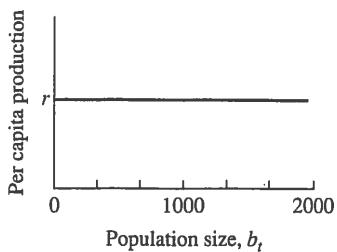
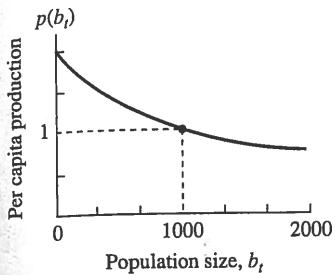


FIGURE 3.3.40

Constant per capita production

**Table 3.3.3**

Population, $b_t$	Per Capita Production, $p(b_t)$
10	1.980
100	1.818
500	1.333
1000	1.000
1500	0.800
2000	0.667



**FIGURE 3.3.41**  
Decreasing per capita production

the real-life situation more faithfully, we have to make sure that it accounts for the reduced per capita production caused by increases in population. In other words, we need to replace the constant  $r$  with an appropriately chosen decreasing function.

Researchers in population dynamics use all kinds of functions for this purpose. We will discuss one of them in the context of logistic growth in Chapter 6. Here, we consider the function

$$p(b_t) = \frac{2}{1 + 0.001b_t}$$

To get a better feel for  $p$ , we build a table of values (Table 3.3.3) and sketch its graph (Figure 3.3.41).

This is what we are looking for—larger populations have smaller per capita production. So, using

$$\text{new population} = \text{per capita production} \times \text{old population}$$

we obtain

$$b_{t+1} = \left( \frac{2}{1 + 0.001b_t} \right) b_t$$

where  $b_0$ , as usual, denotes the initial population. This dynamical system is an example of a model for **limited population**. Through a sequence of examples, we now investigate this model.

### Example 3.3.3

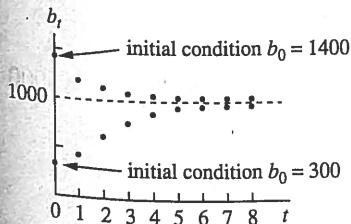
Model for Limited Population: Sample Calculations

Assume that we start with  $b_0 = 300$ . Then

$$b_1 = \left( \frac{2}{1 + 0.001b_0} \right) b_0 = \left( \frac{2}{1 + 0.001(300)} \right) (300) \approx 461.54$$

$$b_2 = \left( \frac{2}{1 + 0.001b_1} \right) b_1 \approx \left( \frac{2}{1 + 0.001(461.54)} \right) (461.54) \approx 631.58$$

and so on:



**FIGURE 3.3.42**  
Limited population with two different initial conditions

$$\begin{aligned} b_3 &\approx 774.19 \\ b_4 &\approx 872.73 \\ b_5 &\approx 932.04 \\ b_6 &\approx 964.82 \\ b_7 &\approx 982.10 \\ b_8 &\approx 990.97 \\ b_9 &\approx 995.46 \end{aligned}$$

Thus, the population increases, but—unlike in the case of exponential growth we studied before—there seems to be a limit to the growth (looking at the numbers, we see that this limit could be 1000; see Figure 3.3.42).

Starting with initial condition  $b_0 = 1400$ , we get

$$b_1 = \left( \frac{2}{1 + 0.001b_0} \right) b_0 = \left( \frac{2}{1 + 0.001(1400)} \right) (1400) \approx 1166.67$$

$$b_2 = \left( \frac{2}{1 + 0.001b_1} \right) b_1 \approx \left( \frac{2}{1 + 0.001(1166.67)} \right) (1166.67) \approx 1076.92$$

and

$$b_3 \approx 1037.04$$

$$b_4 \approx 1018.18$$

$$b_5 \approx 1009.01$$

$$b_6 \approx 1004.48$$

$$b_7 \approx 1002.24$$

In this case the population decreases, and again, it seems to be approaching 1000; see Figure 3.3.42. 

### Example 3.3.4

Model for Limited Population: Equilibria

In order to calculate the equilibria for the discrete-time dynamical system

$$b_{t+1} = \left( \frac{2}{1 + 0.001b_t} \right) b_t$$

we solve the equation

$$b^* = \left( \frac{2}{1 + 0.001b^*} \right) b^*$$

for  $b^*$ . We bring both terms to the same side and factor:

$$b^* - \left( \frac{2}{1 + 0.001b^*} \right) b^* = 0$$

$$b^* \left( 1 - \frac{2}{1 + 0.001b^*} \right) = 0$$

Thus,  $b^* = 0$  or

$$1 - \frac{2}{1 + 0.001b^*} = 0$$

$$\frac{2}{1 + 0.001b^*} = 1$$

$$1 + 0.001b^* = 2$$

after cross-multiplying. It follows that

$$0.001b^* = 1$$

and so

$$b^* = \frac{1}{0.001} = 1000$$

We conclude that there are two equilibria:  $b^* = 0$  represents extinction, and  $b^* = 1000$  represents the population whose per capita production is

$$p(1000) = \frac{2}{1 + 0.001(1000)} = 1$$

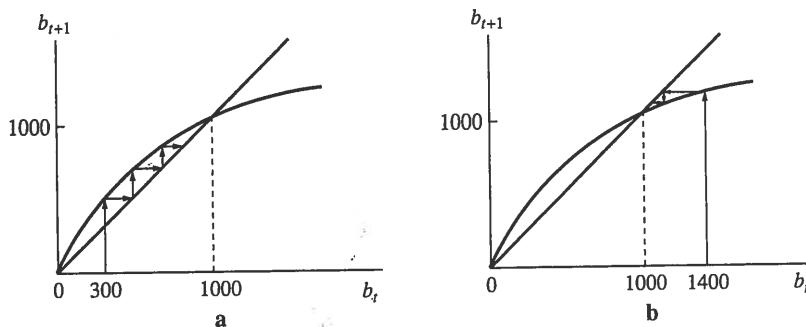
In other words, each bacterium produces one new bacterium, so the population just breaks even (remains constant at 1000). 

**Example 3.3.5** Model for Limited Population: Cobwebbing

To fully understand our model, we investigate it geometrically. Using a graphing device, we produce the graph of the updating function

$$f(b_t) = \left( \frac{2}{1 + 0.001b_t} \right) b_t$$

in Figure 3.3.43. Cobwebbing confirms our earlier conjectures: starting with  $b_0 = 300$ , the solution increases and approaches 1000 (Figure 3.3.43a). The solution with initial condition  $b_0 = 1400$  decreases and approaches 1000 as well (Figure 3.3.43b). Note that  $b_0 = 0$  is an unstable equilibrium, whereas  $b_0 = 1000$  is stable.  $\blacksquare$

**FIGURE 3.3.43**

Cobwebbing the limited population model

## Dynamics of Alcohol Use

Using our knowledge of dynamical systems, we now build a model for the consumption and elimination of alcohol, so that we can understand better how it works and how it affects people who consume it.

To construct our model, we need to understand how the human body processes alcohol. In the case of caffeine, the body tends to eliminate a *fixed proportion* (about 13% per hour), no matter what the amount. Thus, if we have 200 mg of caffeine in our body, 26 mg will be eliminated within an hour. If we have twice as much caffeine (400 mg), then  $0.13(400 \text{ mg}) = 52 \text{ mg}$  (i.e., twice as much) will be eliminated over the next hour.

The elimination of alcohol is different: neither the amount that breaks down per hour nor the proportion is constant. It has been determined that the amount of alcohol that is broken down (eliminated) by the liver depends on the amount of alcohol present in the body. The larger the amount, the smaller the proportion of alcohol that is eliminated.

For the model and for subsequent calculations, we have to define a unit of alcohol. By a commonly accepted definition, one drink contains 14 g of alcohol, which is equivalent to 1.5 oz (44 mL) of 80-proof alcohol (vodka, rum, tequila, etc.), 5 oz (144 mL) of white wine, or 12 oz (355 mL) of beer.

By  $a_t$  we denote the amount of alcohol (in grams) at time  $t$ . Let  $r(a_t)$  be the rate of elimination of alcohol (percent per hour) at the moment when the amount of alcohol in the body is  $a_t$ . Consider the function (derived from experimental data)

$$r(a_t) = \frac{10.1}{4.2 + a_t}$$

where  $a_t \geq 5.9$  g. For values of  $a_t$  smaller than 5.9 g, the rate  $r(a_t)$  is bigger than 1 (more than 100% per hour), which does not make sense. Note that  $r(a_t)$  is very similar to the per capita production function we studied in the limited growth population model.

To understand  $r(a_t)$  better, we calculate a few values:

Amount of Alcohol, $a_t$ , in Grams	Rate of Elimination, $r(a_t)$
6	0.9902
7	0.9012
14	0.5550
28	0.3137
42	0.2186
70	0.1361

Looking at the values, we see that we managed to do what we needed: smaller amounts of alcohol correspond to larger elimination rates, and vice versa. More precisely, if the body contains 14 g of alcohol (equivalent to one drink), it will be able to eliminate 55.5% of it within one hour (of course assuming that no new alcohol is introduced into the body). However, if someone has three rapid drinks (i.e., consumes 42 g of alcohol), then only 21.86% of the 42 g of alcohol will be eliminated within one hour.

Note that 55.5% of 14 g is 7.8 g; as well, 31.37% of 28 g is 8.8 g and 21.86% of 42 g is 9.2 g. So—as a ball-park, for a reasonable range of  $a_t$ —the net elimination is about 8 g to 9 g of alcohol per hour.

Now we are ready to build the model. If  $a_t$  is the current amount of alcohol in the body, what will  $a_{t+1}$  be?

The amount of alcohol eliminated is equal to

$$\text{amount of alcohol} \times \text{elimination rate}$$

i.e.,

$$a_t r(a_t) = a_t \left( \frac{10.1}{4.2 + a_t} \right) = \frac{10.1 a_t}{4.2 + a_t}$$

So the amount of alcohol still present in the body is

$$\text{amount at time } t - \text{eliminated amount}$$

i.e.,

$$a_t - \frac{10.1 a_t}{4.2 + a_t}$$

So, because  $a_{t+1}$  is

$$\text{amount still present} + (\text{possibly new amount})$$

we get

$$a_{t+1} = a_t - \frac{10.1 a_t}{4.2 + a_t} + d$$

where  $d$  is the amount of alcohol consumed between times  $t$  and  $t + 1$ . (Actually, to be precise,  $d$  is the amount of alcohol consumed right at the end of the hour—since we did not incorporate it into the part that the body eliminates in the one-hour interval.)

This formula represents the dynamics of the elimination and consumption of alcohol. In the following examples we examine a few scenarios.

### Example 3.3.6

Dynamics of Alcohol: Half a Drink per Hour

Assume that a student has two rapid drinks and then decides to consume half a drink every hour. What will the long-term effects be?

The initial condition (two rapid drinks) is  $a_0 = 28$  g, and  $d = 7$  g (or half a drink every hour). The corresponding discrete-time dynamical system is

$$a_{t+1} = a_t - \frac{10.1 a_t}{4.2 + a_t} + 7$$

where  $t$  is time in hours.

In a moment we will calculate a solution. But first, let us try to figure out  $a_1$  without the above formula. The initial amount of alcohol in the body is 28 g. Looking at the table, we see that, with that amount of alcohol present, the elimination rate is 31.37% per hour. So,  $0.3137(28) \approx 8.7836$  g of alcohol will be eliminated in an hour, and the amount still left in the body is  $28 \text{ g} - 8.7836 \text{ g} \approx 19.2164$  g. Adding half a drink (7 g), we obtain that, at the end of the hour, the body contains 26.2164 g of alcohol.

To confirm this, and to calculate the solution, we use the model:

$$a_1 = a_0 - \frac{10.1a_0}{4.2 + a_0} + 7 = 28 - \frac{10.1(28)}{4.2 + 28} + 7 \approx 26.2174$$

The difference between this value and the one we obtained earlier is due to round-off error. Similarly, we get

$$a_2 = a_1 - \frac{10.1a_1}{4.2 + a_1} + 7 \approx 26.2174 - \frac{10.1(26.2174)}{4.2 + 26.2174} + 7 \approx 24.5120$$

and

$$a_3 \approx 22.8894$$

$$a_4 \approx 21.3553$$

$$a_5 \approx 19.9152$$

$$a_6 \approx 18.5743$$

So, the total amount of alcohol decreases, in spite of the fact that the student consumes half a drink every hour. How is this possible?

Since there is a relatively small amount of alcohol present, the body manages to eliminate all of the new alcohol (the half-drink every hour), as well as some of the alcohol left from the initial consumption.

Next, we calculate the equilibrium, and then, using cobwebbing, show that the above solution will approach it.

We start from

$$a^* = a^* - \frac{10.1a^*}{4.2 + a^*} + 7$$

subtract  $a^*$  from both sides, and rearrange terms:

$$\frac{10.1a^*}{4.2 + a^*} = 7$$

Now, cross-multiply and solve:

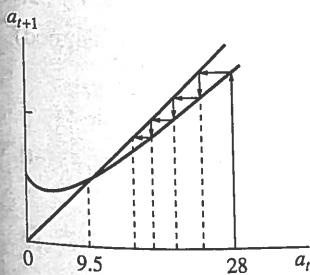
$$10.1a^* = 29.4 + 7a^*$$

$$3.1a^* = 29.4$$

$$a^* = \frac{29.4}{3.1} \approx 9.5$$

Cobwebbing (see Figure 3.3.44) shows that the above solution decreases toward the equilibrium of approximately 9.5 g.

As well—making use of the cobweb diagram again—we see that if the student starts with a small amount of alcohol in the body (less than 9.5 g), or no alcohol at all, the routine of consuming half a drink every hour will increase the alcohol content, but only to the limit of 9.5 g. (Thus,  $a^* \approx 9.5$  is a stable equilibrium.) ▲



**FIGURE 3.3.44**  
Cobwebbing alcohol consumption model (horizontal axis not to scale)

### Example 3.3.7 Dynamics of Alcohol: One Drink per Hour

The system

$$a_{t+1} = a_t - \frac{10.1a_t}{4.2 + a_t} + 14$$

with  $a_0 = 14$  describes the scenario where a person starts with one drink, and then keeps consuming one drink per hour.

Let us try to find an equilibrium. We start with

$$a^* = a^* - \frac{10.1a^*}{4.2 + a^*} + 14$$

then subtract  $a^*$  from both sides and rearrange terms:

$$\frac{10.1a^*}{4.2 + a^*} = 14$$

Next, cross-multiply and solve:

$$10.1a^* = 58.8 + 14a^*$$

$$-3.9a^* = 58.8$$

$$a^* \approx -15.1$$

Although mathematically correct, the equilibrium of  $-15.1$  does not make sense in the context of this application.

Let us calculate a solution:  $a_0 = 14$  and so

$$a_1 = a_0 - \frac{10.1a_0}{4.2 + a_0} + 14 = 14 - \frac{10.1(14)}{4.2 + 14} + 14 \approx 20.2308$$

Similarly,

$$a_2 \approx 25.8671$$

$$a_3 \approx 31.1779$$

$$a_4 \approx 36.2770$$

$$a_5 \approx 41.2250$$

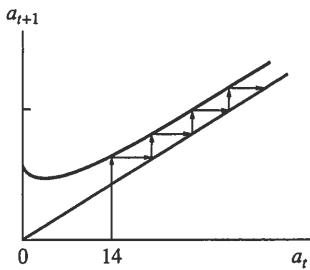


FIGURE 3.3.45

Cobwebbing alcohol consumption model

So the amount of alcohol will increase: after five hours, the total amount in the body will be almost equal to the consumption of three drinks (42 g).

Cobwebbing (see Figure 3.3.45) confirms that the consumption of one drink per hour will keep increasing the amount of alcohol in the body.

We have seen that continuous consumption of half a drink every hour will make the alcohol content in the body stabilize at a low amount (9.5 g). However, the one-drink-per-hour routine will keep increasing the alcohol level. ■

### Example 3.3.8

Dynamics of Alcohol: Pure Elimination

Suppose that a person decides to stop drinking at the moment when the alcohol in their body reaches 60 g. How long will it take to eliminate almost all of the alcohol (so that there is less than 1 g left)?

The initial condition is  $a_0 = 60$  g, and  $d = 0$  g (since no new alcohol is consumed). The corresponding dynamical system is

$$a_{t+1} = a_t - \frac{10.1a_t}{4.2 + a_t}$$

Starting with  $a_0 = 60$ , we compute

$$a_1 = a_0 - \frac{10.1a_0}{4.2 + a_0} = 60 - \frac{10.1(60)}{4.2 + 60} \approx 50.56$$

$$a_2 \approx 41.23$$

$$a_3 \approx 32.07$$

$$a_4 \approx 23.14$$

$$a_5 \approx 14.59$$

$$a_6 \approx 6.75$$

$$a_7 \approx 0.52$$

So, after seven hours, there will be approximately 0.52 g of alcohol left unabsorbed in the body. Note that  $a_8 = -0.59$ , which does not make sense. 

**Summary** In this section, we investigated several models: **unlimited population growth** and decay, **limited population growth**, and **dynamics of consumption of two drugs**: caffeine and alcohol. Although ideal and generalized in many ways, the models nevertheless provide us with useful insights into the real-life situations they describe.

### 3.3 Exercises

#### Mathematical Techniques

► 1-3 ■ Find each population.

1. If  $b_{t+1} = 1.3b_t$  and  $b_0 = 12,000$ , find  $b_8$ .
2. If  $b_{t+1} = 1.01b_t$  and  $b_0 = 100$ , find  $b_{500}$ .
3. If  $b_{t+1} = 0.99b_t$  and  $b_0 = 100$ , find  $b_{500}$ .

► 4-5 ■ Assume that the population changes according to  $b_{t+1} = rb_t$ . Find the per capita production,  $r$ , and the initial population,  $b_0$ , given the following measurements.

4.  $b_1 = 6$  and  $b_3 = 600$ .
5.  $b_2 = 2000$  and  $b_3 = 3000$ .

► 6-8 ■ Find the per capita production for an exponentially changing population.

6. The population increased from 100 to 400 in 4 months (in units of new members per member per month).
7. The population increased from 1200 to 400,000 in 25 years (in units of new members per member per year).
8. The population decreased from one million to one thousand in one year (in units of new members per member per year).
9. Consider a population that changes according to  $p_{t+1} = rp_t(1 - p_t)$ , where  $r > 1$  is a constant. Identify the per capita production, and describe its graph in words. Find the equilibrium population.
10. Population A increased from 125,000 to 313,000 in two months. Population B increased from 2500 to 9000 in three months. Assuming that both populations change exponentially, which one has the larger per capita production?

► 11-14 ■ Consider the model for limited population,

$$b_{t+1} = \frac{12}{1 + 0.001b_t} b_t$$

11. Let  $b_0 = 1000$ . Using a calculator or a computer, find  $b_1, b_2, b_3, b_4$ , and  $b_5$ . What value do these numbers approach?
12. Let  $b_0 = 20,000$ . Using a calculator or a computer, find  $b_1, b_2, b_3, b_4$ , and  $b_5$ . What value do these numbers approach?
13. Calculate the equilibria and explain their meaning.
14. Using cobwebbing, show that the population that starts at  $b_0 = 12,000$  will decrease toward one of the equilibrium points calculated in Exercise 13.

► 15-18 ■ Consider the alcohol consumption model

$$a_{t+1} = a_t - \frac{10.1a_t}{4.2 + a_t} + d$$

where  $d$  is the constant amount of alcohol that is consumed every hour.

15. If  $a_0 = 42$  g and  $d = 7$  g, find  $a_5$  and give an interpretation.
16. If  $a_0 = 0$  g and  $d = 28$  g, find  $a_5$  and give an interpretation.
17. If  $a_0 = 28$  g and  $d = 14$  g, find  $a_5$  and give an interpretation.
18. If there are 50 g of alcohol in the body and no new alcohol is consumed, how long will it take for the alcohol level to fall below 1 g?
19. Find all equilibria of the population whose per capita production is given by  $\frac{rp_t}{1 + p_t^2}$ , where  $r > 0$ .

#### Applications

► 20-23 ■ Find the solution of each discrete-time dynamical system, express it in exponential notation, and solve for when the given time reaches the given target. Sketch the graph of the solution.

20. A population follows the discrete-time dynamical system  $b_{t+1} = rb_t$ , with  $r = 1.5$  and  $b_0 = 10^6$ . When will the population reach  $10^7$ ?
21. A population follows the discrete-time dynamical system  $b_{t+1} = rb_t$ , with  $r = 1.2$  and  $b_0 = 10^6$ . When will the population reach  $10^7$ ?
22. A population follows the discrete-time dynamical system  $b_{t+1} = rb_t$ , with  $r = 1.01$  and  $b_0 = 10^6$ . When will the population reach  $10^7$ ?
23. A population follows the discrete-time dynamical system  $b_{t+1} = rb_t$ , with  $r = 0.9$  and  $b_0 = 10,000$ . When will the population reach 1,000?
24. Consider the dynamical system (Beverton-Holt recruitment curve)

$$n_{t+1} = \frac{rn_t}{1 + (r - 1)n_t/k}$$

where  $k > 0$ ,  $r > 1$ , and  $n_t$  represents some population.

- a. Find all meaningful equilibria.
- b. Let  $k = 90$  and  $r = 10$ , and assume that  $n_0 = 30$ . Compute the first four values of  $n_t$  and plot them on a graph. Next, assume that  $n_0 = 120$ . Compute the first four values of  $n_t$  and plot them on the same graph. Based on your numerical experiment, give a possible interpretation of the constant  $k$ .

25. We modify the dynamical system  $b_{t+1} = rb_t$  by replacing the constant per capita production rate with a decreasing function different from the one we studied in Examples 3.3.3–3.3.5. To be specific, we assume that the ratio  $b_{t+1}/b_t$  starts (i.e., when  $t=0$ ) at some value  $r > 1$  and decreases as the reciprocal of a linear function until it reaches 1 when  $t=N$ .

- a. Write (for convenience, consider the reciprocal)

$$\frac{b_t}{b_{t+1}} = \alpha b_t + \beta$$

Using the fact that  $b_0/b_1 = 1/r$  and  $b_N/b_{N+1} = 1$ , find  $\alpha$  and  $\beta$ .

- b. Let  $K = b_N = b_{N+1}$ . Show that

$$b_{t+1} = \frac{r(K - b_0)b_t}{K - rb_0 + (r - 1)b_t}$$

This model is one version of the Beverton-Holt discrete-time population model.

26. Another variant of the Beverton-Holt population model is given by

$$b_{t+1} = \frac{rb_t}{1 + \frac{1}{M}b_t}$$

where  $r > 1$  and  $M$  is a positive constant.

- a. Show that the solution of the system is given by

$$b_t = \frac{(r-1)Mb_0}{b_0 + ((r-1)M - b_0)r^{-t}}$$

- b. We have not formally introduced limits. However, try to justify the fact that, as  $t$  increases,  $b_t$  approaches  $(r-1)M$ . The quantity  $(r-1)M$  is called the *carrying capacity* of the environment.

- 27–29 ■ If the number of individuals falls below a certain critical number,  $m$ , the population faces extinction (since it is no longer capable of avoiding the damaging effects of inbreeding and is unable to cope with changes in the environment). Calculate the time when the following populations will fall to the level that will threaten their survival. Assume that the per capita production rate is constant in each case.

27. The population of black rhinoceroses in Africa was 2500 in 1993 and 2410 in 2004. It has been estimated that  $m=500$ .
28. In 1990, there were about 5000 southern mountain caribou in British Columbia. In 2009, only about 1900 remained. The critical number is  $m=500$ .
29. In 2005, there were about 25,000 Beluga whales in Western Hudson Bay. (This estimate is based on aerial surveys conducted by Fisheries and Oceans Canada. The surveys could not detect submerged whales, so the actual number of whales could be significantly higher.) Facing losses due to hunting and pollution, the population is believed to be decreasing, although its exact size is hard to estimate. Suppose that a more recent estimate (year 2010) is 24,000 whales. Take the minimum survival to be  $m=200$ .

- 30–33 ■ Assume that the dynamics of caffeine absorption is given by  $c_{t+1} = 0.87c_t + d$ , where  $t$  is time in hours and  $d$  is the amount of caffeine taken every hour.

30. If the initial amount of caffeine is  $c_0 = 1000$  mg (equivalent to five to six double espressos!) and no new caffeine is consumed, estimate the time needed for 90% of the caffeine to be eliminated from the body (i.e., 10% left).
31. If the initial amount of caffeine is  $c_0 = 600$  mg and no new caffeine is consumed, estimate the time needed for 50% of the caffeine to be eliminated from the body.
32. If the initial amount of caffeine is  $c_0 = 40$  mg and every hour we consume a small coffee (60 mg of caffeine), will the total amount of caffeine in our body increase or decrease? Find the equilibrium amount of caffeine.
33. Let  $c_0 = 100$  mg and  $d = 120$  mg. Find the equilibrium. How long will it take for the caffeine to reach 90% of the equilibrium?
34. Consider the alcohol consumption model

$$a_{t+1} = a_t - \frac{10.1a_t}{4.2 + a_t} + d$$

where  $d$  is the constant amount that is consumed every hour. For which values of  $d$  is there an equilibrium? For which values is there no equilibrium?

### Computer Exercises

35. Population A follows the dynamics  $a_{t+1} = 1.3a_t$  with  $a_0 = 100$ . Population B can be described by  $b_{t+1} = 1.1b_t$  with  $b_0 = 1000$ .
- Which population is larger when  $t = 10$ ?
  - Which population reaches 3000 first?
  - When does population A become larger than population B?
  - When does population A reach 1 million?
  - What is the size of population A when population B reaches 1 million?

36. Consider the model for limited population,

$$b_{t+1} = \frac{10.4}{1 + 0.0005b_t} b_t$$

where  $t$  is time in years.

- What is the positive equilibrium value?
- Let  $b_0 = 2000$ . How many years will it take for the population to reach 95% of the equilibrium value?
- Let  $b_0 = 2000$ . How many years will it take for the population to come within 1% of the equilibrium value?
- Let  $b_0 = 100,000$ . Comment on the rate at which the population will approach the equilibrium. In reality, what could possibly cause this kind of change?

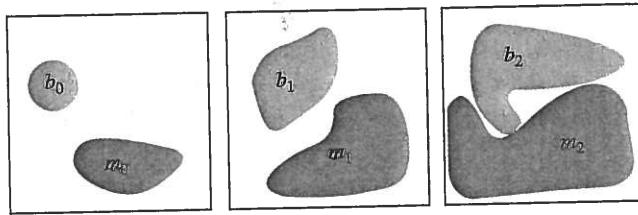
## 3.4

## Nonlinear Dynamics Model of Selection

Some discrete-time dynamical systems we have studied so far (bacterial populations, caffeine, tree height, and mite populations) are said to be **linear** because the updating function is linear. We now derive a model of two competing bacterial populations that leads naturally to a discrete-time dynamical system that is not linear. **Nonlinear dynamical systems** can have much more complicated behaviour than linear systems, as we witnessed working with the limited growth model. For example, they may have more than one equilibrium. By comparing the two equilibria in this model of selection, we will catch another glimpse of an important theme of this book, the **stability** of equilibria.

### A Model of Selection

Our original model of bacterial growth followed the population of a single type of bacterium, denoted by  $b_t$  at time  $t$ . Suppose that a mutant type with population  $m_t$  appears and begins competing. If the original type (or **wild type**) has a per capita production of 1.5 and the mutant type has a per capita production of 2 (Figure 3.4.46), the two populations will follow the discrete-time dynamical systems



**FIGURE 3.4.46**

An invasion by mutant bacteria

$$\begin{aligned} b_{t+1} &= 1.5b_t && \text{discrete-time dynamical system for wild type} \\ m_{t+1} &= 2m_t && \text{discrete-time dynamical system for mutants} \end{aligned} \quad (3.4.1)$$

The per capita production of the mutant type is greater than that of the wild type, perhaps because it is better able to survive. Over time, we would expect the population to include a larger and larger proportion of mutant bacteria. The establishment of this mutant is an example of **selection**. Selection occurs when the frequency of a genetic type changes over time.

Imagine observing this mixed population for many hours. Counting all of the bacteria each hour would be impossible. Nonetheless, we could track the mutant invasion by taking a sample and measuring the fraction of the mutant type by counting or using a specific stain. If this fraction became larger and larger, we would know that the mutant type was taking over.

How can we model the dynamics of the fraction? The vital first step is to define a new variable. In this case, we set  $p_t$  to be the fraction (or the percent) of mutants at time  $t$ . Then

$$\begin{aligned} p_t &= \frac{\text{number of mutants}}{\text{total number of bacteria}} \\ &= \frac{\text{number of mutants}}{\text{number of mutants} + \text{number of wild type}} \\ &= \frac{m_t}{m_t + b_t} \end{aligned} \quad (3.4.2)$$

In other words, we think of  $p_t$  as the percent of mutants relative to the total population of bacteria.

What is the fraction (percent) of the wild type? It is the number of wild type divided by the total number of bacteria, or

$$\begin{aligned}\text{fraction (percent) of wild type} &= \frac{\text{number of wild type}}{\text{total number of bacteria}} \\ &= \frac{\text{number of wild type}}{\text{number of mutants} + \text{number of wild type}} \\ &= \frac{b_t}{m_t + b_t}\end{aligned}$$

Note that

$$\text{fraction of mutants} + \text{fraction of wild type} = \frac{m_t}{m_t + b_t} + \frac{b_t}{m_t + b_t} = 1$$

as it should—because all bacteria are of one of these two types, the fractions must add up to 1 (i.e., 100%). Thus,

$$\begin{aligned}\text{fraction of mutants} &= p_t = \frac{m_t}{m_t + b_t} \\ \text{fraction of wild type} &= 1 - p_t = \frac{b_t}{m_t + b_t}\end{aligned}\tag{3.4.3}$$

### Example 3.4.1 Finding the Fractions of Mutants and Wild Type

Assume that  $b_t = 3 \cdot 10^6$  and  $m_t = 2 \cdot 10^5$ . The total number of bacteria is  $b_t + m_t = 3.2 \cdot 10^6$ , and the fraction of the mutant type is

$$p_t = \frac{m_t}{m_t + b_t} = \frac{2 \cdot 10^5}{3.2 \cdot 10^6} = 0.0625.$$

Thus, mutant bacteria represent 6.25% of the total population. The fraction of the wild type is

$$\frac{b_t}{m_t + b_t} = \frac{3 \cdot 10^6}{3.2 \cdot 10^6} = 0.9375.$$

We conclude that the wild bacteria represent 93.75% of the total population of bacteria. Clearly,

$$\text{fraction of mutants} + \text{fraction of wild type} = 0.0625 + 0.9375 = 1$$



Our goal is to express  $p_{t+1}$  in terms of  $p_t$ , i.e., to find a formula that relates the fraction of the mutant type one hour later to the present fraction of the mutant type. We consider an example first.

### Example 3.4.2 Finding an Updated Fraction

Recall that, with  $b_t = 3 \cdot 10^6$  and  $m_t = 2 \cdot 10^5$  as in Example 3.4.1, the fraction of mutants is  $p_t = 0.0625$ .

The updated populations are

$$\begin{aligned}m_{t+1} &= 2m_t = 4 \cdot 10^5 \\ b_{t+1} &= 1.5b_t = 4.5 \cdot 10^6\end{aligned}$$

The updated fraction of the mutant type,  $p_{t+1}$ , is

$$p_{t+1} = \frac{4 \cdot 10^5}{4 \cdot 10^5 + 4.5 \cdot 10^6} \approx 0.0816$$

As expected, the fraction has increased. We might expect that the fraction of mutants would increase by a factor equal to the ratio  $\frac{2}{1.5} \approx 1.333$  of the per capita productions of the two types. In fact,

$$\frac{p_{t+1}}{p_t} = \frac{0.0816}{0.0625} \approx 1.3056$$

which is slightly less. We will soon see why the mutant increases more slowly than we might at first expect. ▲

We follow these same steps to find the discrete-time dynamical system for  $p_t$ . By definition, the fraction of mutants is

$$p_{t+1} = \frac{m_{t+1}}{m_{t+1} + b_{t+1}}$$

Using the discrete-time dynamical systems for the two types (Equation 3.4.1), we find

$$p_{t+1} = \frac{2m_t}{2m_t + 1.5b_t} \quad (3.4.4)$$

Although mathematically correct, this is not a satisfactory discrete-time dynamical system. We have supposed that the actual values of  $m_t$  and  $b_t$  are impossible to measure. The discrete-time dynamical system must give the new fraction,  $p_{t+1}$ , in terms of the old fraction,  $p_t$ , which we can measure by sampling.

We can do this by using an algebraic trick: dividing the numerator and the denominator by the same thing. Because the definition of  $p_t$  has the total population  $m_t + b_t$  in the denominator, we divide it into the numerator and denominator, finding

$$p_{t+1} = \frac{\frac{2m_t}{m_t + b_t}}{\frac{2m_t}{m_t + b_t} + 1.5 \frac{b_t}{m_t + b_t}}$$

We can simplify by substituting

$$p_t = \frac{m_t}{m_t + b_t}$$

(Equation 3.4.2) and

$$1 - p_t = \frac{b_t}{m_t + b_t}$$

(Equation 3.4.3), thus finding

$$p_{t+1} = \frac{2p_t}{2p_t + 1.5(1 - p_t)} \quad (3.4.5)$$

This is the discrete-time dynamical system we sought, giving a formula for the fraction at time  $t + 1$  in terms of the fraction at time  $t$ .

### Example 3.4.3 Using the Discrete-Time Dynamical System to Find the Updated Fraction

If  $p_t = 0.0625$ , as in Example 3.4.1, the discrete-time dynamical system tells us that

$$p_{t+1} = \frac{2 \cdot 0.0625}{2 \cdot 0.0625 + 1.5(1 - 0.0625)} \approx 0.0816$$

This matches the answer we found before but is based only on *measurable quantities*. ▲

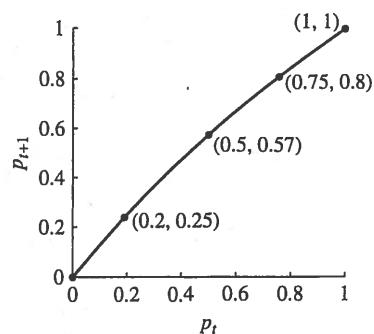


FIGURE 3.4.47

Graph of updating function from the selection model

This calculation illustrates one of the great strengths of mathematical modelling. Our *derivation* of this measurable discrete-time dynamical system used the values  $m_t$  and  $b_t$ , which are impossible to measure. But just because things cannot be measured in practice does not mean they cannot be measured in principle. These values do exist, and they can be worked with mathematically. One can think of mathematical models as a way to see the invisible.

The discrete-time dynamical system for the fraction (Equation 3.4.5) is not linear because it involves division. The graph of the function is curved (Figure 3.4.47). We drew it by plotting points: taking the values for the fraction  $p_t$  (which must lie between 0 and 1), we obtained the points  $(0, 0)$ ,  $(0.2, 0.25)$ ,  $(0.5, 0.57)$ ,  $(0.75, 0.8)$ , and  $(1, 1)$  on the graph.

To find the equilibria, we simplify Equation 3.4.5 first:

$$p_{t+1} = \frac{2p_t}{2p_t + 1.5(1 - p_t)} = \frac{2p_t}{2p_t + 1.5 - 1.5p_t} = \frac{2p_t}{0.5p_t + 1.5}$$

Now from

$$p^* = \frac{2p^*}{0.5p^* + 1.5}$$

we get

$$p^* - \frac{2p^*}{0.5p^* + 1.5} = 0$$

$$p^* \left( 1 - \frac{2}{0.5p^* + 1.5} \right) = 0$$

Therefore,  $p^* = 0$  or

$$\frac{2}{0.5p^* + 1.5} = 1$$

$$0.5p^* + 1.5 = 2$$

$$0.5p^* = 0.5$$

and so  $p^* = 1$ . These equilibria correspond to extinction of the mutant (at  $p^* = 0$ ) and extinction of the wild type (at  $p^* = 1$ ).

## The Discrete-Time Dynamical System and Equilibria

We can gain a better understanding of this process by studying the general case. Suppose that the mutant type has per capita production  $s$  and the wild type has per capita production  $r$  (Figure 3.4.48). The populations follow

$$\begin{aligned} m_{t+1} &= sm_t \\ b_{t+1} &= rb_t \end{aligned} \tag{3.4.6}$$

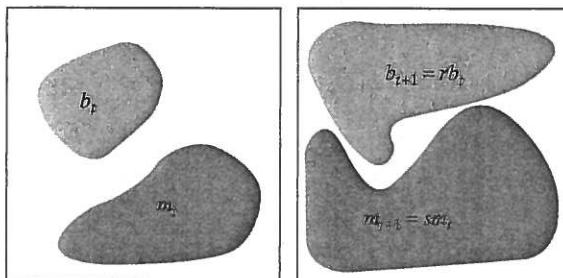


FIGURE 3.4.48

The general case

We can follow the steps above to derive the discrete-time dynamical system for the fraction:

$$\begin{aligned} p_{t+1} &= \frac{m_{t+1}}{m_{t+1} + b_{t+1}} \\ &= \frac{sm_t}{sm_t + rb_t} \\ &= \frac{s \frac{m_t}{m_t + b_t}}{s \frac{m_t}{m_t + b_t} + r \frac{b_t}{m_t + b_t}} \\ &= \frac{sp_t}{sp_t + r(1 - p_t)} \end{aligned}$$

This gives the general form

$$p_{t+1} = \frac{sp_t}{sp_t + r(1 - p_t)} \quad (3.4.7)$$

#### **Example 3.4.4** Substituting Parameters into the General Discrete-Time Dynamical System

The derivation in the previous subsection considered the case  $s = 2$  and  $r = 1.5$ . Substituting these parameter values into the general form for bacterial selection gives

$$p_{t+1} = \frac{2p_t}{2p_t + 1.5(1 - p_t)}$$

matching what we found before. ▲

The updating function for the general model (3.4.7) is given by

$$f(p_t) = \frac{sp_t}{sp_t + r(1 - p_t)} = \frac{sp_t}{r + (s - r)p_t}$$

Consider the case  $s > r$  (i.e., the mutants have higher per capita production than the wild type). Note that  $f(0) = 0$  and  $f(1) = 1$ ; see Figure 3.4.49a. Because (keep in mind that  $p_t \leq 1$ )

$$r + (s - r)p_t \leq r + (s - r) = s$$

we conclude that

$$f(p_t) = \frac{sp_t}{r + (s - r)p_t} \geq \frac{sp_t}{s} = p_t$$

Consequently, the graph of the updating function lies above the diagonal except at the intersection points,  $p_t = 0$  and  $p_t = 1$ , as shown in Figure 3.4.49 (the plot was obtained using a graphing device). This means that any value of  $p_t$  between 0 and 1 will be increased by the discrete-time dynamical system, consistent with the higher per capita production of the mutants. The cobwebbing moves up, indicating this increase (Figure 3.4.49b).

**Note** What we just said is true because the updating function has positive slope. If the updating function lies above the diagonal but has negative slope, then the solution is not increasing (see Example 3.2.6).

What happens if the per capita production of the wild type exceeds that of the mutants? With  $r = 2.1$  and  $s = 1.7$ , the dynamical system is

$$p_{t+1} = \frac{1.7p_t}{1.7p_t + 2.1(1 - p_t)}$$

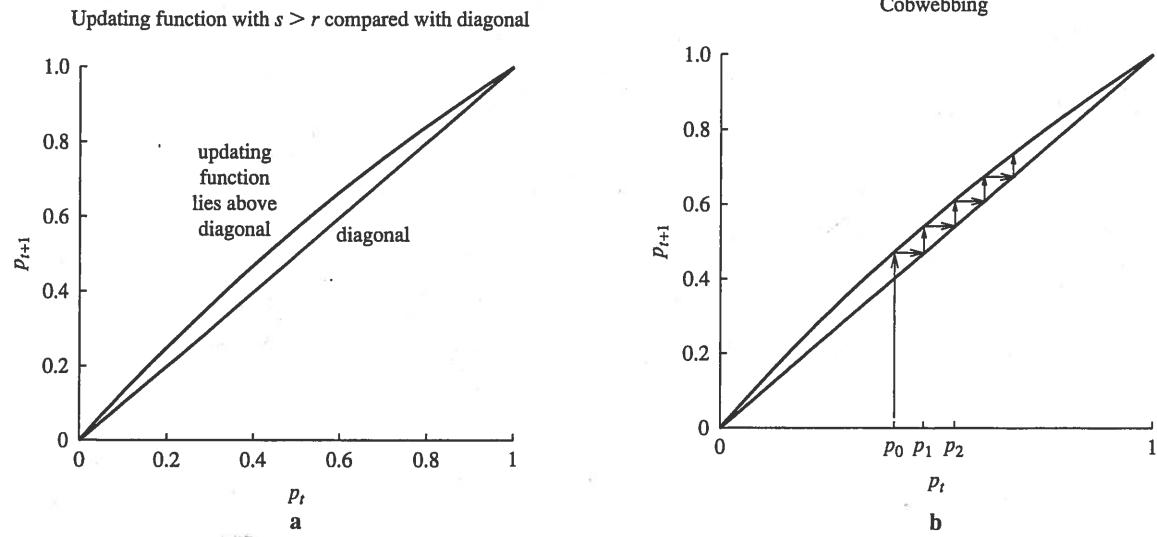


FIGURE 3.4.49

Dynamics when mutants reproduce more quickly

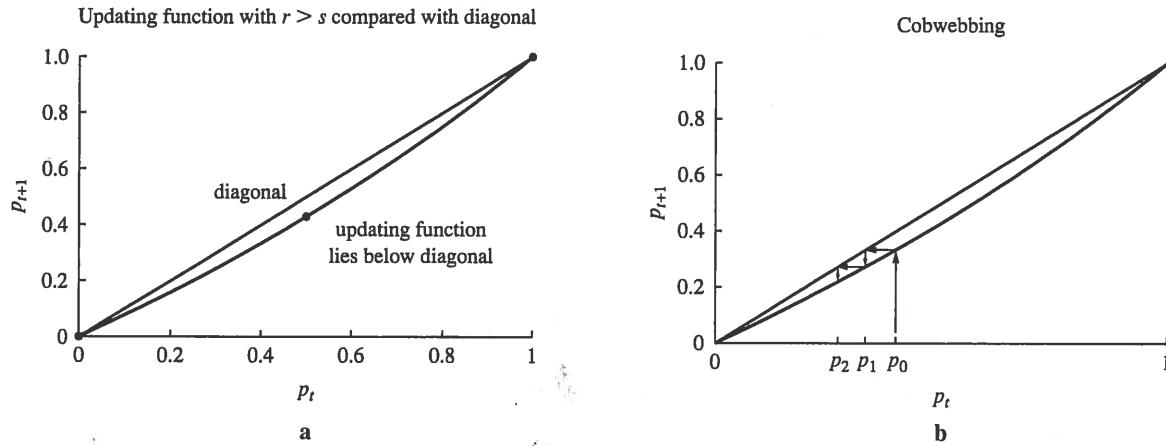


FIGURE 3.4.50

Dynamics when the wild type reproduces more quickly

The points  $(0, 0)$ ,  $(0.5, 0.45)$ , and  $(1, 1)$  lie on the graph, which itself lies below the diagonal (Figure 3.4.50a). Values of  $p_t$  between 0 and 1 are decreased by the discrete-time dynamical system, as shown by the decreasing cobweb (Figure 3.4.50b). This is consistent with the lower production of the mutants.

Finally, what happens if the two types have equal per capita production? If  $r=s$ , the discrete-time dynamical system simplifies to

$$\begin{aligned}
 p_{t+1} &= \frac{sp_t}{sp_t + s(1-p_t)} \\
 &= \frac{sp_t}{sp_t + s - sp_t} \\
 &= \frac{sp_t}{s} \\
 &= p_t
 \end{aligned}$$

In this case, the discrete-time dynamical system leaves all values unchanged. When both types reproduce equally well, the fraction of the mutant neither increases nor

decreases, and every value of  $p_t$  is an equilibrium. This makes biological sense; there is no selection in this case. This does not say that the *total number* of bacteria is unchanged; if  $r = s = 2$ , the total number will double each hour. The *fraction* of mutants remains the same.

We now solve the general system

$$p_{t+1} = \frac{sp_t}{sp_t + r(1 - p_t)}$$

for the equilibria. Start from

$$p^* = \frac{sp^*}{sp^* + r(1 - p^*)}$$

move all terms to the left, expand, and factor:

$$\begin{aligned} p^* - \frac{sp^*}{sp^* + r(1 - p^*)} &= 0 \\ p^* \left( 1 - \frac{s}{sp^* + r(1 - p^*)} \right) &= 0 \end{aligned}$$

Thus,  $p^* = 0$  or

$$\begin{aligned} \frac{s}{sp^* + r(1 - p^*)} &= 1 \\ sp^* + r(1 - p^*) &= s \end{aligned}$$

Again, move all terms to the left and factor:

$$\begin{aligned} sp^* + r(1 - p^*) - s &= 0 \\ sp^* + r - rp^* - s &= 0 \\ p^*(s - r) - (s - r) &= 0 \\ (s - r)(p^* - 1) &= 0 \end{aligned}$$

We conclude that either  $s = r$  or  $p^* = 1$ .

What do these three equilibria mean? If  $s = r$ , the discrete-time dynamical system leaves all values unchanged, and every value of  $p_t$  is an equilibrium. Otherwise, the equilibria are  $p^* = 0$  and  $p^* = 1$ . When  $p^* = 0$ , the population consists entirely of the wild type. Because our model includes no mutation or immigration, there is nowhere for the mutant type to arise. Similarly, when  $p^* = 1$  the population consists entirely of the mutant type, and the wild type will never arise. These equilibria correspond to the extinction equilibrium for a population of one type of bacteria: at  $p^* = 0$  the mutants are extinct, and at  $p^* = 1$  the wild type are extinct.

Figure 3.4.51 shows many steps of cobwebbing with  $s = 2$  and  $r = 1.5$ , starting near the equilibrium  $p^* = 0$ . The solution moves slowly away from 0, moves swiftly through the halfway point at  $p_t = 0.5$ , and then slowly approaches the other equilibrium at  $p_t = 1$ .

If we started *exactly* at  $p_0 = 0$ , the solution would remain at  $p_t = 0$  for all times  $t$ . Similarly, if we started *exactly* at  $p_0 = 1$ , the solution would remain at  $p_t = 1$  for all times  $t$ . The two equilibria behave quite differently, however, if our starting point is nearby. A solution starting *near*  $p^* = 0$  moves steadily *away from* the equilibrium (Figure 3.4.51). A solution starting *near*  $p^* = 1$  moves *toward* the equilibrium (Figure 3.4.52). Thus,  $p^* = 0$  is an unstable equilibrium and  $p^* = 1$  is a stable equilibrium.

We will derive powerful methods to analyze discrete-time dynamical systems and determine whether their equilibria are stable or unstable. Because these techniques require the derivative, a central idea from calculus, we must first study the foundational notions of limits and rate of change.

### Summary

As an example of a **nonlinear dynamical system**, a discrete-time dynamical system with a curved graph, we derived the equation for the fraction of mutants invading a

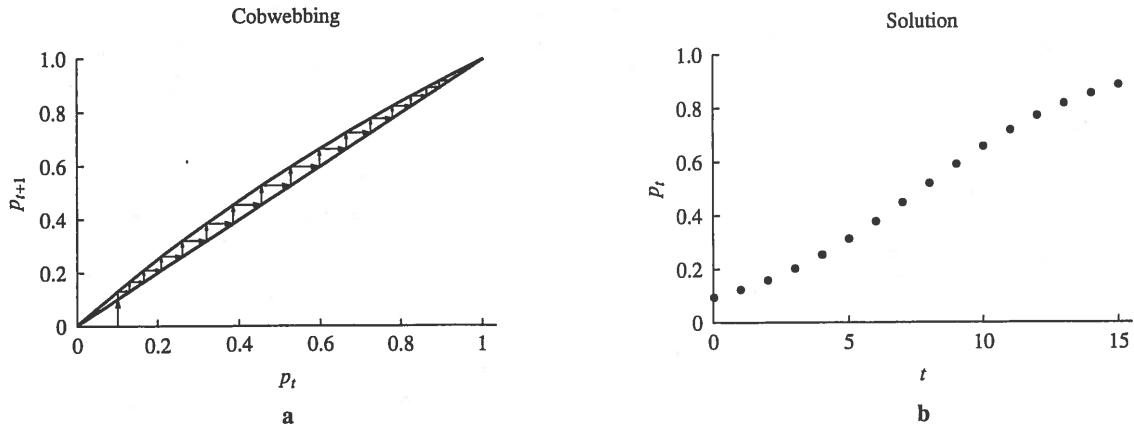


FIGURE 3.4.51

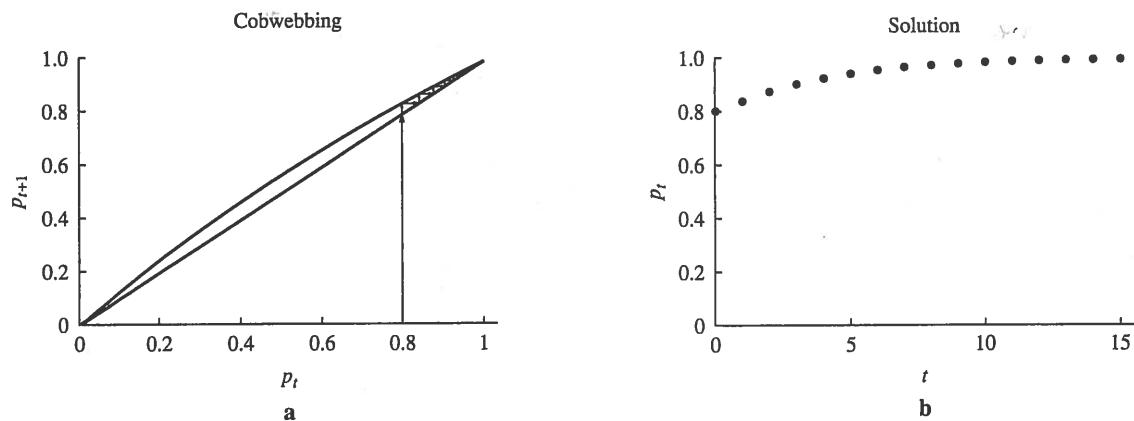
Solution of the selection model starting near  $p_0 = 0$ 

FIGURE 3.4.52

Solution of the selection model starting near  $p_0 = 1$ 

population of wild type bacteria. This dynamical system, unlike the linear ones studied hitherto, has two equilibria. One of these equilibria is **unstable**; solutions starting nearby move farther and farther away. The other is **stable**; solutions starting nearby move closer and closer to the equilibrium.

## 3.4 Exercises

### Mathematical Techniques

- 1–4 ■ A population consists of 200 red birds and 800 blue birds. Find the fraction of red birds and blue birds after the following. Check that the fractions add up to 1.

- The population of red birds doubles and the population of blue birds remains the same.
- The population of blue birds doubles and the population of red birds remains the same.
- The population of red birds is multiplied by a factor of  $r$  and the population of blue birds remains the same.
- The population of blue birds is multiplied by a factor of  $s$  and the population of red birds remains the same.

- 5–6 ■ Sketch graphs of the following functions.

5.  $f(x) = \frac{x}{x+1}$  for  $0 \leq x \leq 2$ .

6.  $g(x) = \frac{3x}{2x+1}$  for  $0 \leq x \leq 2$ .

- 7–10 ■ Using the discrete-time dynamical system and the derivation of Equation 3.4.7, find  $p_t$ ,  $m_{t+1}$ ,  $b_{t+1}$ , and  $p_{t+1}$  in each situation.

7.  $s = 1.2$ ,  $r = 2$ ,  $m_t = 1.2 \cdot 10^5$ ,  $b_t = 3.5 \cdot 10^6$

8.  $s = 1.2$ ,  $r = 2$ ,  $m_t = 1.2 \cdot 10^5$ ,  $b_t = 1.5 \cdot 10^6$

9.  $s = 0.3$ ,  $r = 0.5$ ,  $m_t = 1.2 \cdot 10^5$ ,  $b_t = 3.5 \cdot 10^6$

10.  $s = 1.8$ ,  $r = 1.8$ ,  $m_t = 1.2 \cdot 10^5$ ,  $b_t = 3.5 \cdot 10^6$

► 11–12 ■ Solve for the equilibria of each discrete-time dynamical system.

11.  $p_{t+1} = \frac{p_t}{p_t + 2(1 - p_t)}$

► 12.  $p_{t+1} = \frac{4p_t}{4p_t + 0.5(1 - p_t)}$

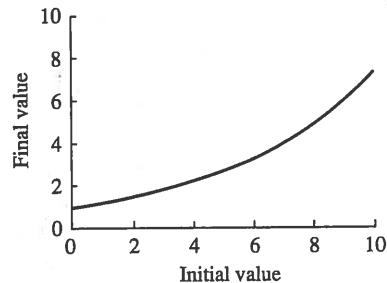
► 13–14 ■ Find all non-negative equilibria of the following mathematically elegant discrete-time dynamical systems.

13.  $x_{t+1} = \frac{x_t}{1 + ax_t}$ , where  $a$  is a positive parameter. What happens to this system if  $a = 0$ ?

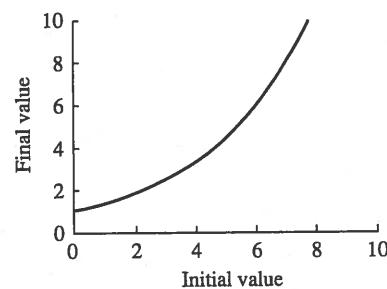
14.  $x_{t+1} = \frac{x_t}{a + x_t}$ , where  $a$  is a positive parameter. What happens to this system if  $a = 0$ ?

► 15–18 ■ Identify stable and unstable equilibria on the following graphs of updating functions.

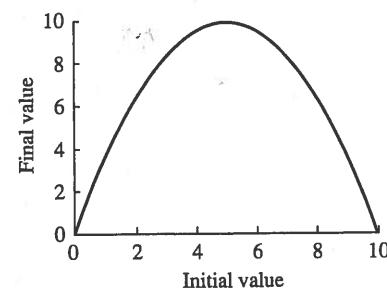
15.



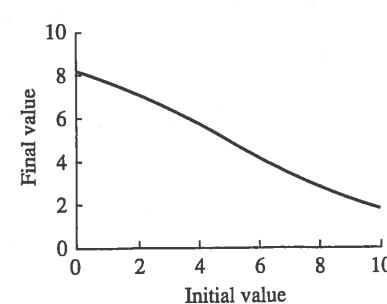
16.



17.



18.



## Applications

► 19–22 ■ Find and graph the updating function for each case of the selection model (Equation 3.4.7). Cobweb starting from  $p_0 = 0.1$  and  $p_0 = 0.9$ . Which equilibria seem to be stable in each case?

19.  $s = 1.2, r = 2$

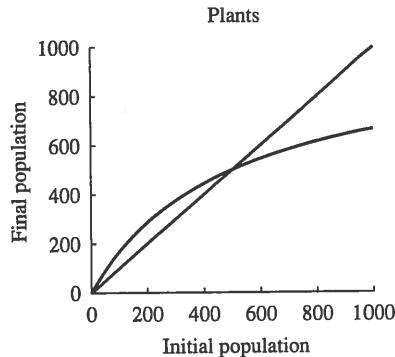
20.  $s = 1.8, r = 0.8$

21.  $s = 0.3, r = 0.5$ . Compare with the result of Exercise 19.

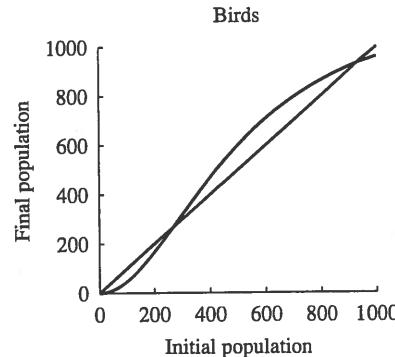
► 22.  $s = 1.8, r = 1.8$

► 23–24 ■ For each discrete-time dynamical system, indicate which of the equilibria are stable and which are unstable.

23.



24.



► 25–28 ■ This section ignores the important evolutionary force of mutation. This series of problems builds models that consider mutation without reproduction. Suppose that 20% of wild type bacteria transform into mutants and that 10% of mutants transform back into wild type (revert). In each case, find the following.

- The number of wild type bacteria that mutate and the number of mutants that revert.
  - The number of wild type bacteria and the number of mutants after mutation and reversion.
  - The total number of bacteria before and after mutation. Why is it the same?
  - The fraction of mutants before and after mutation.
25. Begin with  $1 \cdot 10^6$  wild type and  $1 \cdot 10^5$  mutants.
26. Begin with  $1 \cdot 10^5$  wild type and  $1 \cdot 10^6$  mutants.

27. Begin with  $b_t$  wild type and  $m_t$  mutants. Find the discrete-time dynamical system for the fraction,  $p_t$ , of mutants (divide  $m_{t+1}$  by  $b_{t+1} + m_{t+1}$  to find  $p_{t+1}$  and use the fact that  $b_{t+1} + m_{t+1} = b_t + m_t$ ). Find the equilibrium fraction of mutants. Cobweb starting from the initial condition in Exercise 25. Is the equilibrium stable?

28. Begin with  $b_t$  wild type and  $m_t$  mutants, but suppose that a fraction 0.1 mutate and a fraction 0.2 revert. Find the discrete-time dynamical system and the equilibrium fraction of mutants.

► 29–32 ■ This series of problems combines mutation with selection. In one simple scenario, mutations occur in only one direction (wild type turn into mutants but not vice versa), but wild type and mutants have different per capita production. Suppose that a fraction 0.1 of wild type mutate each generation but that each wild type individual produces 2 offspring while each mutant produces only 1.5 offspring. In each case, find the following.

- The number of wild type bacteria that mutate.
- The number of wild type bacteria and the number of mutants after mutation.
- The number of wild type bacteria and the number of mutants after reproduction.
- The total number of bacteria after mutation and reproduction.
- The fraction of mutants after mutation and reproduction.

29. Begin with  $1 \cdot 10^6$  wild type and  $1 \cdot 10^5$  mutants.

30. Begin with  $1 \cdot 10^5$  wild type and  $1 \cdot 10^6$  mutants.

31. Begin with  $b_t$  wild type and  $m_t$  mutants. Find the discrete-time dynamical system for the fraction,  $p_t$ , of mutants. Find the equilibrium fraction of mutants. Cobweb starting from the initial condition in Exercise 29. Is the equilibrium stable?

32. Begin with  $b_t$  wild type and  $m_t$  mutants, but suppose that a fraction 0.2 mutate and that the per capita production of mutants is 1. Find the discrete-time dynamical system and the equilibrium fraction of mutants.

► 33–36 ■ The model of selection studied in this section is similar in many ways to a model of migration. Suppose two adjacent islands have populations of butterflies, with  $x_t$  on the first island and  $y_t$  on the second. Each year, 20% of the butterflies from the first island fly to the second and 30% of the butterflies from the second island fly to the first.

33. Suppose there are 100 butterflies on each island at time  $t=0$ . How many are on each island at  $t=1$ ? At  $t=2$ ?

34. Suppose there are 200 butterflies on the first island and none on the second at time  $t=0$ . How many are on each island at  $t=1$ ? At  $t=2$ ?

35. Find equations for  $x_{t+1}$  and  $y_{t+1}$  in terms of  $x_t$  and  $y_t$ .

36. Divide both sides of the discrete-time dynamical system for  $x_t$  by  $x_{t+1} + y_{t+1}$  to find a discrete-time dynamical system for the fraction  $p_t$  on the first island. What is the equilibrium fraction?

► 37–38 ■ The following two problems extend the migration models to include some reproduction. Each year, 20% of the butterflies from the first island fly to the second and 30% of the butterflies from the second island fly to the first. Again,  $x_t$  represents the number of butterflies on the first island,  $y_t$  represents the number of butterflies on the second island, and  $p_t$  represents the fraction of butterflies on the first island. In each case:

a. Start with 100 butterflies on each island and find the number after migration and after reproduction.

b. Find equations for  $x_{t+1}$  and  $y_{t+1}$  in terms of  $x_t$  and  $y_t$ .

c. Find the discrete-time dynamical system for  $p_{t+1}$  in terms of  $p_t$ .

d. Find the equilibrium,  $p^*$ .

e. Sketch a graph and cobweb from a reasonable initial condition.

37. Each butterfly that begins the year on the first island produces one additional butterfly after migration (whether it finds itself on the first or the second island). Those that begin the year on the second island do not reproduce. No butterflies die.

38. Now suppose that the butterflies that do not migrate reproduce (making one additional butterfly each) and those that do migrate fail to reproduce from exhaustion. No butterflies die.

► 39–42 ■ The model describing the dynamics of the pain medication in the bloodstream,

$$M_{t+1} = 0.5M_t + 1$$

becomes nonlinear if the fraction of medication used is a function of the concentration. In the basic model, half is used no matter how much there is. More generally,

$$\begin{aligned} \text{new concentration} &= \text{old concentration} \\ &- \text{fraction used} \\ &\times \text{old concentration} \\ &+ \text{supplement} \end{aligned}$$

Suppose that the fraction used is a *decreasing function* of the concentration.

39. Suppose that

$$\text{fraction used} = \frac{0.5}{1 + 0.1M_t}$$

Write the discrete-time dynamical system and solve for the equilibrium. Why is the equilibrium larger than the value of  $M^* = 2$  that we found for the basic model?

40. Suppose that

$$\text{fraction used} = \frac{0.5}{1 + 0.4M_t}$$

Write the discrete-time dynamical system and solve for the equilibrium. Why is the equilibrium larger than the value of  $M^* = 2$  that we found for the basic model?

41. Suppose that

$$\text{fraction used} = \frac{\beta}{1 + 0.1M_t}$$

for some parameter  $\beta \leq 1$ . Write the discrete-time dynamical system and solve for the equilibrium. Sketch a graph of the equilibrium as a function of  $\beta$ . Cobweb starting from  $M_0 = 1$  in the cases  $\beta = 0.05$  and  $\beta = 0.5$ .

42. Suppose that

$$\text{fraction used} = \frac{0.5}{1 + \alpha M_t}$$

for some parameter  $\alpha$ . Write the discrete-time dynamical system and solve for the equilibrium. Sketch a graph of the equilibrium as a function of  $\alpha$ . What happens when  $\alpha > 0.5$ ? Can you explain this in biological terms? Cobweb starting from  $M_0 = 1$  in the cases  $\alpha = 0.1$  and  $\alpha = 1$ .

► 43–46 ■ Our models of bacterial population growth neglect the fact that bacteria produce fewer offspring in large populations. The following problems introduce two important models of this process, having the form

$$b_{t+1} = r(b_t)b_t$$

where the per capita production,  $r$ , is a function of the population size,  $b_t$ . In each case:

- Graph the per capita production as a function of population size.
- Write the discrete-time dynamical system and graph the updating function.
- Find the equilibria.
- Cobweb and indicate whether the equilibrium seems to be stable.

43. One widely used nonlinear model of competition is the logistic model, where per capita production is a linearly decreasing function of population size. Suppose that the per capita production is  $r(b) = 2 \left(1 - \frac{b}{1 \cdot 10^6}\right)$ .

44. In an alternative model, the per capita production decreases as the reciprocal of a linear function. Suppose that the per capita production is  $r(b) = \frac{2}{1 + \frac{b}{1 \cdot 10^6}}$ .

45. In another alternative model, called the Ricker model, the per capita production decreases exponentially. Suppose that per capita production is  $r(b) = 2e^{-\frac{b}{1 \cdot 10^6}}$ .

46. In a model with an **Allee effect**, organisms reproduce poorly when the population is small. In one case, per capita production follows  $r(b) = \frac{4b}{1 + b^2}$ .

### Computer Exercises

47. Consider the discrete-time dynamical system

$$x_{t+1} = rx_t(1 - x_t)$$

similar to the form in Exercise 43. Plot the updating function and have a computer find solutions for 50 steps starting from  $x_0 = 0.3$  for the following values of  $r$ :

- Some value of  $r$  between 0 and 1. What is the only equilibrium?
- Some value of  $r$  between 1 and 2. Where are the equilibria? Which one seems to be stable?
- Some value of  $r$  between 2 and 3. Where are the equilibria? Which one seems to be stable?
- Try several values of  $r$  between 3 and 4. What is happening to the solution? Is there any stable equilibrium?
- The solution is chaotic when  $r = 4$ . One property of chaos is **sensitive dependence on initial conditions**. Compare a solution starting from  $x_0 = 0.3$  with one starting at  $x_0 = 0.30001$ . Even though they start off very close, they soon separate and become completely different. Why might this be a problem for a scientific experiment?

48. Consider the equation describing the dynamics of selection (Equation 3.4.7),

$$p_{t+1} = \frac{sp_t}{sp_t + r(1 - p_t)}$$

Suppose you have two cultures, 1 and 2. In 1, the mutant does better than the wild type, and in 2 the wild type does better. In particular, suppose that  $s = 2$  and  $r = 0.3$  in culture 1 and that  $s = 0.6$  and  $r = 2$  in culture 2. Define discrete-time dynamical systems  $f_1$  and  $f_2$  to describe the dynamics in the two cultures.

- Graph the functions  $f_1$  and  $f_2$  along with the identity function. Find the first five values of solutions, starting from  $p_0 = 0.02$  and  $p_0 = 0.98$  in each culture. Explain what each solution is doing and why.
- Suppose you change the experiment. Begin by taking a population with a fraction  $p_0$  of mutants. Split this population in half, and place one half in culture 1 and the other half in culture 2. Let the bacteria reproduce once in each culture, and then mix them together. Split the mix in half and repeat the process. The updating function is

$$f(p) = \frac{f_1(p) + f_2(p)}{2}$$

Can you derive this? Plot this updating function along with the diagonal. Have a computer find the equilibria and label them on your graph. Do they make sense?

- Use cobwebbing to figure out which equilibria are stable.
- Find one solution starting from  $p_0 = 0.001$  and another starting from  $p_0 = 0.999$ . Are these results consistent with the stability of the equilibria? Explain why the solutions do what they do. Why don't they move toward  $p = 0.5$ ?

### 3.5 A Model of Gas Exchange in the Lung

The exchange of materials between an organism and its environment is one of the most fundamental biological processes. By following the amount of chemical step by step through the breathing process, we can derive a discrete-time dynamical system that models this process for a simplified lung. This discrete-time dynamical system describes how the outside air mixes with the internal air, taking the form of a **weighted average**. This model provides a framework we can use to study more complicated biological processes such as the absorption or release of a chemical.

#### A Model of the Lungs

Consider a simplified breathing process. Suppose a lung has a volume of 3 L (litres) when full. With each breath, 0.6 L of the air is exhaled and replaced by 0.6 L of outside (or ambient) air. After exhaling, the volume of the lung is 2.4 L, and it returns to 3 L after inhaling (Figure 3.5.53).

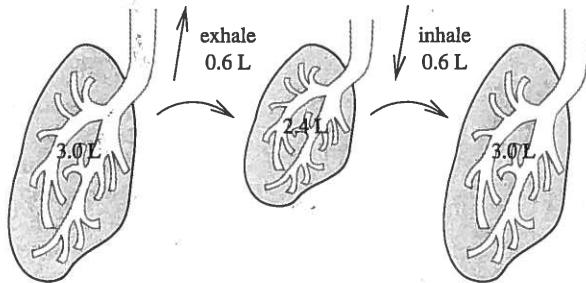
Suppose further that the lung contains a particular chemical with concentration 2 millimoles per litre before exhaling. (A mole is a chemical unit indicating  $6.02 \times 10^{23}$  molecules, and a millimole (mmol) represents  $6.02 \times 10^{20}$  molecules.) The ambient air has a chemical concentration of 5 mmol/L. What is the chemical concentration after one breath?

We must track three quantities through these steps: the volume (Figure 3.5.53), the total amount of chemical, and the chemical concentration (Figure 3.5.54). To find the total amount from the concentration, we use the fundamental relation

$$\text{total amount} = \text{concentration} \times \text{volume}$$

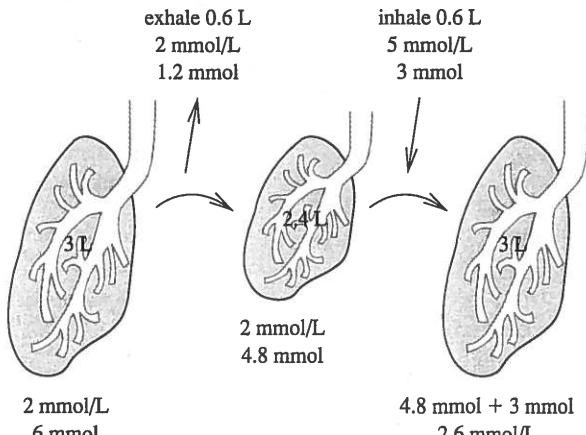
Conversely, to find the concentration from the total amount, we rearrange the fundamental relation to

$$\text{concentration} = \frac{\text{total amount}}{\text{volume}}$$



**FIGURE 3.5.53**

Gas exchange in the lung: the volume



**FIGURE 3.5.54**

Gas exchange in the lung: the concentration

One basic biological assumption underlies our reasoning: the air breathed out has a concentration equal to that of the whole lung. This means that the air in the lung is completely mixed at each breath, which is not exactly true.

Assuming also that neither air nor chemical is produced or used while breathing, we can track the process step by step:

Step	Volume (L)	Total Chemical (mmol)	Concentration (mmol/L)	What We Did
Air in lung before breath	3	6	2	Multiplied volume of lung (3) by concentration (2) to get 6.
Air exhaled	0.6	1.2	2	Multiplied volume exhaled (0.6) by concentration (2) to get 1.2.
Air in lung after exhalation	2.4	4.8	2	Multiplied volume remaining (2.4) by concentration (2) to get 4.8.
Air inhaled	0.6	3	5	Multiplied volume inhaled (0.6) by ambient concentration (5) to get 3.
Air in lung after breath	3	7.8	2.6	Found total by adding 4.8 + 3 = 7.8 and divided by volume (3) to get 2.6.

Let us create a discrete-time dynamical system that will describe the breathing process. From the analysis we just finished, we realize that the original concentration of 2 mmol/L is updated to 2.6 mmol/L after a breath. To write the discrete-time dynamical system, we must figure out the concentration after a breath,  $c_{t+1}$ , as a function of the concentration before the breath,  $c_t$ . We follow the same steps but replace 2 with  $c_t$  (Figure 3.5.55):

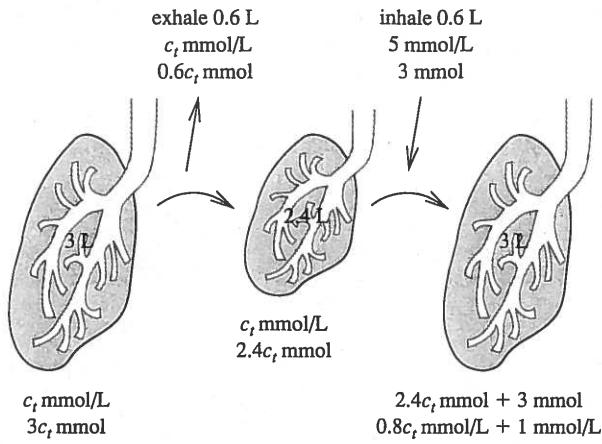
Step	Volume (L)	Total Chemical (mmol)	Concentration (mmol/L)	What We Did
Air in lung before breath	3	$3c_t$	$c_t$	Multiplied volume of lung (3) by concentration ( $c_t$ ) to get $3c_t$ .
Air exhaled	0.6	$0.6c_t$	$c_t$	Multiplied volume exhaled (0.6) by concentration ( $c_t$ ) to get $0.6c_t$ .
Air in lung after exhalation	2.4	$2.4c_t$	$c_t$	Multiplied volume remaining (2.4) by concentration ( $c_t$ ) to get $2.4c_t$ .
Air inhaled	0.6	3	5	Multiplied volume inhaled (0.6) by ambient concentration (5) to get 7.5.
Air in lung after breath	3	$3 + 2.4c_t$	$1 + 0.8c_t$	Found total by adding $3 + 2.4c_t$ and divided by volume (3) to get $1 + 0.8c_t$ .

The discrete-time dynamical system is therefore

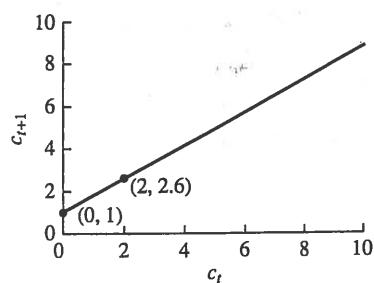
$$c_{t+1} = 1 + 0.8c_t$$

Checking, we find that an input of  $c_t = 2$  gives

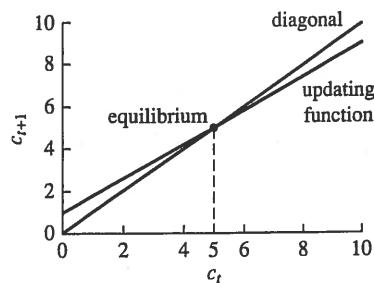
$$c_{t+1} = 1 + 0.8 \cdot 2 = 2.6$$

**FIGURE 3.5.55**

Gas exchange in the lung: finding the discrete-time dynamical system

**FIGURE 3.5.56**

Updating function for the lung model

**FIGURE 3.5.57**

Equilibrium of the lung discrete-time dynamical system

as found above. The graph of the updating function is a line with vertical-intercept 1 and slope 0.8 (Figure 3.5.56).

We can solve for equilibria and use cobwebbing to better understand this discrete-time dynamical system. Let the variable  $c^*$  stand for an equilibrium. The equation for equilibrium says that an input of  $c^*$  is unchanged by the discrete-time dynamical system, or

$$c^* = 1 + 0.8c^*$$

The solutions of this equation are equilibria (Figure 3.5.57). To solve, we write

$$c^* = 1 + 0.8c^*$$

$$c^* - 0.8c^* = 1$$

$$0.2c^* = 1$$

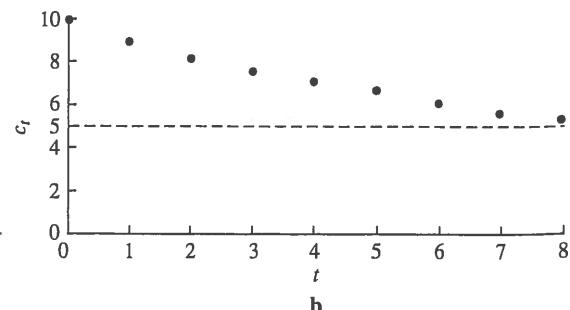
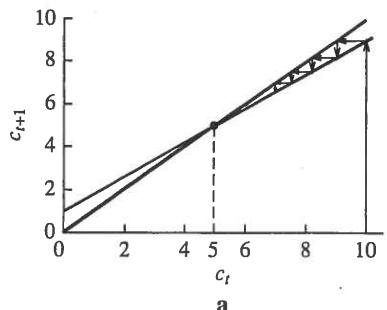
$$c^* = \frac{1}{0.2} = 5$$

The equilibrium value is 5 mmol/L. We can check this by plugging  $c_t = 5$  into the discrete-time dynamical system, finding

$$c_{t+1} = 1 + 0.8 \cdot 5 = 5$$

A concentration of 5 is indeed unchanged by the breathing process.

We can use cobwebbing to check whether solutions move toward or away from this equilibrium. Recall that cobwebbing is a graphical procedure for finding approximate solutions. Both the cobweb starting from  $c_0 = 10$  (Figure 3.5.58) and the one starting from  $c_0 = 0$  (Figure 3.5.59) produce solutions that approach the equilibrium at  $c^* = 5$ . Thus, the breathing process forces the concentration to stabilize: no matter what its initial value, over time, the concentration will approach 5 mmol/L (which is the concentration of the ambient air that is breathed in). In other words, the equilibrium,  $c^* = 5$ , is stable.

**FIGURE 3.5.58**

Cobwebbing the lung discrete-time dynamical system:  $c_0 = 10$

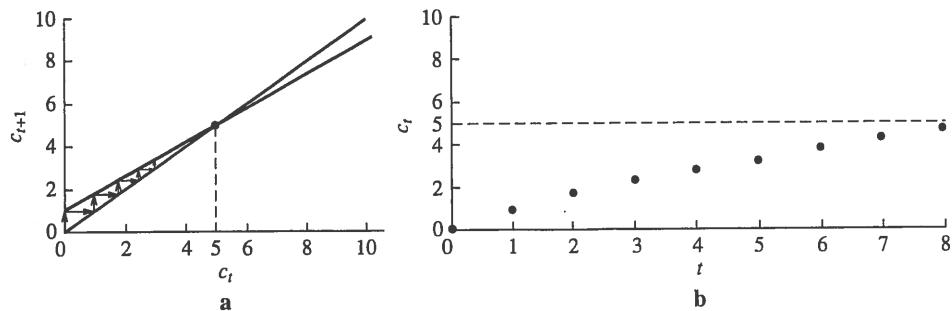


FIGURE 3.5.59

Cobwebbing the lung discrete-time dynamical system:  $c_0 = 0$

## The Lung System in General

In the previous subsection, we assumed that the lung had a volume of 3 L, that 0.6 L of air was exhaled and inhaled, and that the ambient concentration of chemical was 5 mmol/L. Suppose, more generally, that the lung has a volume of  $V$  litres, that  $W$  litres of air is exhaled and inhaled at each breath, and that the ambient concentration of chemical is  $\gamma$  (mmol/L). Our goal is to find the discrete-time dynamical system giving  $c_{t+1}$  as a function of  $c_t$ , which we can do by again following the breathing process step by step (Figure 3.5.60):

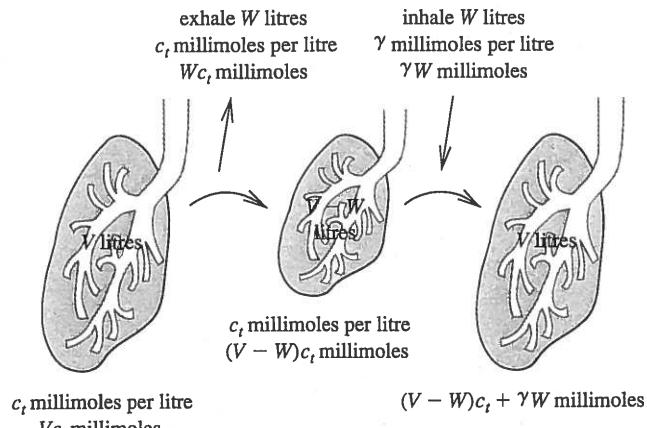
Step	Volume (L)	Total Chemical (mmol)	Concentration (mmol/L)	What We Did
Air in lung before breath	$V$	$c_t V$	$c_t$	Multipled volume of lung ( $V$ ) by concentration ( $c_t$ ) to get $c_t V$ .
Air exhaled	$W$	$c_t W$	$c_t$	Multipled volume exhaled ( $W$ ) by concentration ( $c_t$ ) to get $c_t W$ .
Air in lung after exhalation	$V - W$	$c_t(V - W)$	$c_t$	Multipled volume remaining ( $V - W$ ) by concentration ( $c_t$ ) to get $c_t(V - W)$ .
Air inhaled	$W$	$\gamma W$	$\gamma$	Multipled volume inhaled ( $W$ ) by ambient concentration ( $\gamma$ ) to get $\gamma W$ .
Air in lung after breath	$V$	$c_t(V - W) + \gamma W$	$\frac{c_t(V - W) + \gamma W}{V}$	Found total by adding $c_t(V - W)$ to $\gamma W$ and then divided by volume ( $V$ ).

The new concentration appears at the end of the last line of the table, giving the discrete-time dynamical system

$$c_{t+1} = \frac{c_t(V - W) + \gamma W}{V}$$

This equation can be simplified by multiplying out the first term and dividing out the  $V$ :

$$\begin{aligned} c_{t+1} &= \frac{c_t(V - W) + \gamma W}{V} \\ &= \frac{c_t V - c_t W + \gamma W}{V} \end{aligned}$$

**FIGURE 3.5.60**

Gas exchange in the lung: general case

$$= c_t - c_t \frac{W}{V} + \gamma \frac{W}{V}$$

The two values  $W$  (volume of exhaled air) and  $V$  (volume of the lung) appear only as the ratio  $\frac{W}{V}$ , which is the fraction of the total volume exchanged at each breath. For example, when  $W = 0.6$  L and  $V = 3$  L, then  $\frac{W}{V} = 0.2$ , which means that 20% of air is exhaled with each breath. Defining a new parameter

$$q = \frac{W}{V} = \text{fraction of air exchanged}$$

we write the discrete-time dynamical system as

$$c_{t+1} = c_t - c_t q + \gamma q$$

or, after combining terms with  $c_t$ , as **the general lung discrete-time dynamical system**,

$$c_{t+1} = (1 - q)c_t + q\gamma \quad (3.5.1)$$

### Example 3.5.1 Finding the Discrete-Time Dynamical System with Specific Parameter Values

In the original example,  $W = 0.6$  and  $V = 3$ , giving  $q = \frac{W}{V} = 0.2$ . Using  $\gamma = 5$ , the general equation matches our original discrete-time dynamical system because

$$c_{t+1} = (1 - 0.2)c_t + 0.2 \cdot 5 = 0.8c_t + 1$$

Let us think a bit more about the meaning of the parameter  $q$  in the general lung dynamical system

$$c_{t+1} = (1 - q)c_t + q\gamma$$

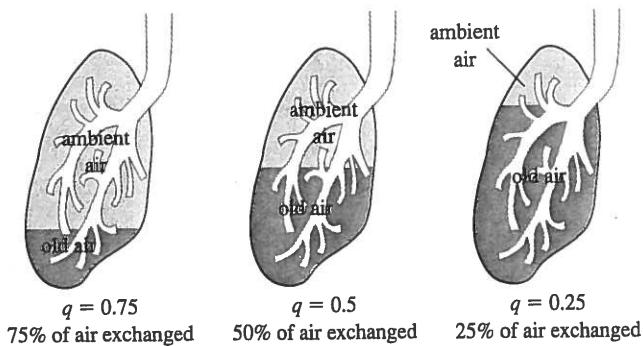
After a breath, the air in the lung is a mix of old air and ambient air (Figure 3.5.61). The fraction  $1 - q$  is old air that remains in the lung, and the remaining fraction,  $q$ , is ambient air. If  $q = 0.5$ , half of the air in the lung after a breath came from outside, and from

$$c_{t+1} = \frac{1}{2}c_t + \frac{1}{2}\gamma$$

we conclude that  $c_{t+1}$  is the average of the previous concentration and the ambient concentration.

If  $q$  is small, little of the internal air is replaced with ambient air, and  $c_{t+1}$  is close to  $c_t$ . If  $q$  is near 1, most of the internal air is replaced with ambient air. The air in the lung then resembles ambient air, and  $c_{t+1}$  is close to the ambient concentration,  $\gamma$ .

The right-hand side of the lung equation is an example of a **weighted average**.



**FIGURE 3.5.61**  
Effects of different values of  $q$

### Definition 3.5.1

A weighted average of two values,  $x$  and  $y$  (which places the weight  $q$  on  $x$  and the weight  $1 - q$  on  $y$ ), is the sum of the form  $qx + (1 - q)y$  for some value of  $q$  between 0 and 1.

When  $q = 1/2$ , the weighted average is the ordinary average. The concentration in the lung after breathing is a weighted average: the fraction  $1 - q$  of air is left over from the previous breath, and the fraction  $q$  is ambient air.

### Example 3.5.2 Weighted Average

Suppose  $x = 2$  and  $y = 5$ . Then the weighted average that places a weight  $q = 0.8$  on  $x$  and a weight  $1 - q = 0.2$  on  $y$  is

$$qx + (1 - q)y = 0.8 \cdot 2 + 0.2 \cdot 5 = 2.6$$

Less weight is placed on  $y$ , and the weighted average is closer to  $x$ .

### Example 3.5.3 Contrasting Weighted Average

Suppose  $x = 2$  and  $y = 5$ , as in Example 3.5.2. The weighted average that places a weight  $q = 0.2$  on  $x$  and a weight  $1 - q = 0.8$  on  $y$  is

$$qx + (1 - q)y = 0.2 \cdot 2 + 0.8 \cdot 5 = 4.4$$

More weight is placed on  $y$ , and the weighted average is closer to  $y$ .

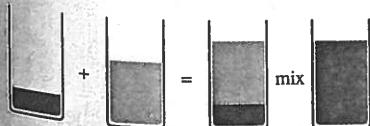
### Example 3.5.4 Ordinary Average

Suppose  $x = 2$  and  $y = 5$ , as in Examples 3.5.2 and 3.5.3. The ordinary average places equal weights  $q = 0.5$  on  $x$  and  $1 - q = 0.5$  on  $y$ , and is equal to

$$qx + (1 - q)y = 0.5 \cdot 2 + 0.5 \cdot 5 = 3.5$$

This value is exactly halfway between  $x$  and  $y$ .

### Example 3.5.5 Weighted Average Applied to Liquids



**FIGURE 3.5.62**  
Mixing liquids as a weighted average

Suppose 1 L of liquid with a concentration of 10 mmol/L of salt is mixed with 3 L of liquid with a concentration of 5 mmol/L of salt (Figure 3.5.62). What is the concentration of the resulting mixture? We can think of this as a weighted average. The 4 L of the mixture contains 1 L of the high-salt solution (or a fraction of 0.25) and 3 L of the low-salt solution (or a fraction of 0.75). The resulting concentration is the weighted average

$$0.25 \cdot 10 \frac{\text{mmol}}{\text{L}} + 0.75 \cdot 5 \frac{\text{mmol}}{\text{L}} = 6.25 \frac{\text{mmol}}{\text{L}}$$

We could work this out explicitly by computing the total amount of salt and the total volume. There are 10 mmol of salt from the first solution and 15 mmol from the

second (multiplying the concentration of 5 mmol/L by the volume of 3 L), for a total of 25 mmol in 4 L. The concentration is

$$\frac{25 \text{ mmol}}{4 \text{ L}} = 6.25 \text{ mmol/L}$$

The weighted average provides perhaps a simpler way to find this answer.

### Example 3.5.6

#### Weighted Average with More Than Two Components

Weighted averages also work when more than two solutions are mixed. Suppose 1 L of liquid with a concentration of 10 mmol/L of salt is mixed with 3 L of liquid with a concentration of 5 mmol/L of salt and 1 L of liquid with a concentration of 2 mmol/L of salt. What is the concentration of the resulting mixture? In this case, the 5-L mixture is composed of 20% (or 0.20) of the high-salt solution, 60% (or 0.60) of the medium-salt solution, and 20% (or 0.20) of the low-salt solution. The resulting concentration is the weighted average

$$0.20 \cdot 10 \text{ mmol/L} + 0.60 \cdot 5 \text{ mmol/L} + 0.20 \cdot 2 \text{ mmol/L} = 5.4 \text{ mmol/L}$$

If we work this out explicitly, there is a total of 10 mmol from the first solution, 15 mmol from the second, and 2 mmol from the last, for a total of 27 mmol in the 5-L mixture. The concentration is

$$\frac{27 \text{ mmol}}{5 \text{ L}} = 5.4 \text{ mmol/L}$$

**The Equilibrium of the Lung Discrete-Time Dynamical System** The general discrete-time dynamical system for the lung model is

$$c_{t+1} = (1 - q)c_t + q\gamma$$

Following the steps for finding equilibria gives

$$\begin{aligned} c^* &= (1 - q)c^* + q\gamma \\ c^* &= c^* - qc^* + q\gamma \\ qc^* - q\gamma &= 0 \\ q(c^* - \gamma) &= 0 \\ q = 0 \text{ or } c^* &= \gamma \end{aligned}$$

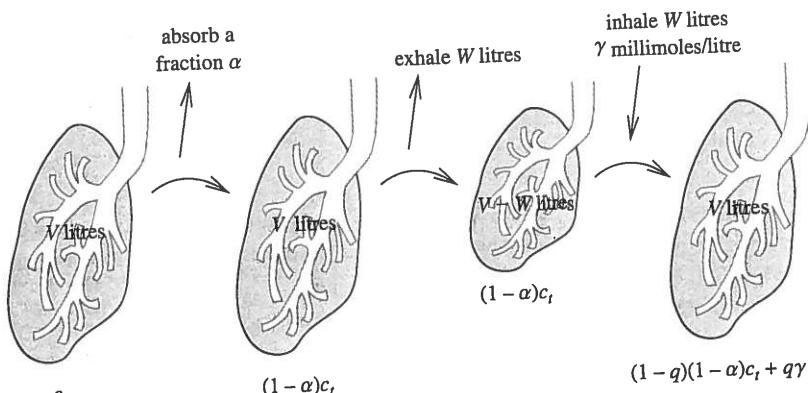
What do these results mean? The first case,  $q = 0$ , occurs when no air is exchanged. Because there is no expression for  $c^*$  in this case, *any* value of  $c_t$  is an equilibrium. This makes sense because a lung that is exchanging no air is, in fact, at equilibrium.

The second case is more interesting. It says that the equilibrium value of the concentration is equal to the ambient concentration. Exchanging air with the outside world has no effect when the inside and the outside match. Doing the calculation in general explains why the equilibrium of 5 mmol/L found earlier in this section must match the ambient concentration of 5 mmol/L.

## Lung Dynamics with Absorption

Our model of chemical dynamics in the lung ignored any absorption of the chemical by the body. We can now consider the dynamics of oxygen, which is in fact absorbed by blood. How will this change the discrete-time dynamical system and the resulting solution and equilibrium?

We can use the weighted average to derive the discrete-time dynamical system describing absorption. Suppose that a fraction,  $q$ , of air is exchanged each breath, that ambient air has a concentration of  $\gamma$ , and that a fraction,  $\alpha$ , of oxygen is absorbed before breathing out (Figure 3.5.63). After absorption, the concentration in the lung is



**FIGURE 3.5.63**  
Dynamics of a lung with absorption

$(1 - \alpha)c_t$ . Mixing produces a weighted average with a fraction  $1 - q$  of this old air and a fraction  $q$  of ambient air, giving the discrete-time dynamical system

$$c_{t+1} = (1 - q)(1 - \alpha)c_t + q\gamma$$

If  $\alpha = 0$ , this reduces to the original model of a lung without absorption.

### Example 3.5.7

#### Absorption of Oxygen by the Lung

Consider again a lung that has a volume of 3 L and that replaces 0.6 L at each breath with ambient air (as in Figure 3.5.54). Suppose now that we are tracking oxygen with an ambient concentration of 21%. Assume that 30% of the oxygen in the lung is absorbed at each breath. We then have

$$q = 0.2$$

$$\alpha = 0.3$$

$$\gamma = 0.21$$

The discrete-time dynamical system is then

$$c_{t+1} = 0.8 \cdot 0.7c_t + 0.2 \cdot 0.21 = 0.56c_t + 0.042$$

The equilibrium concentration in the lung solves

$$c^* = 0.56c^* + 0.042$$

$$0.44c^* = 0.042$$

$$c^* \approx 0.095$$

The equilibrium concentration of oxygen in the lung, which is equal to the concentration of oxygen in the air breathed out, is about 9.5%, or less than half the ambient concentration. □

As a consequence of absorption, the equilibrium concentration will be lower than the ambient concentration. By solving for the equilibrium of the system in general, we can investigate how the equilibrium depends on the fraction absorbed. To find the equilibrium, we solve

$$c^* = (1 - q)(1 - \alpha)c^* + q\gamma$$

$$c^* - (1 - q)(1 - \alpha)c^* = q\gamma$$

$$c^*(1 - (1 - q)(1 - \alpha)) = q\gamma$$

$$c^* = \frac{q\gamma}{1 - (1 - q)(1 - \alpha)}$$

As a check, if we substitute  $\alpha = 0$ , we find

$$c^* = \frac{q\gamma}{1 - (1 - q)} = \frac{q\gamma}{q} = \gamma$$

matching the equilibrium in the case of no absorption.

**Example 3.5.8** The Equilibrium Concentration of Oxygen as a Function of  $\alpha$ 

With the parameter values  $q = 0.2$  and  $\gamma = 0.21$ , we find

$$c^* = \frac{0.2 \cdot 0.21}{1 - 0.8(1 - \alpha)} = \frac{0.042}{1 - 0.8(1 - \alpha)}$$

By substituting values of  $\alpha$  ranging from  $\alpha = 0$  to  $\alpha = 1$ , we can plot the equilibrium concentration as a function of absorption (Figure 3.5.64). ▲

**Example 3.5.9**

Finding  $\alpha$  from the Equilibrium Concentration of Oxygen

Suppose that the actual oxygen concentration in exhaled air is approximately 15%. What fraction of oxygen is in fact absorbed? We can find this by solving for the value of  $\alpha$  that produces  $c^* = 0.15$ :

$$0.15 = \frac{0.042}{1 - 0.8(1 - \alpha)}$$

$$0.15(1 - 0.8(1 - \alpha)) = 0.042$$

$$0.15(0.2 + 0.8\alpha) = 0.042$$

$$0.2 + 0.8\alpha = \frac{0.042}{0.15} = 0.28$$

$$0.8\alpha = 0.08$$

$$\alpha = 0.1$$

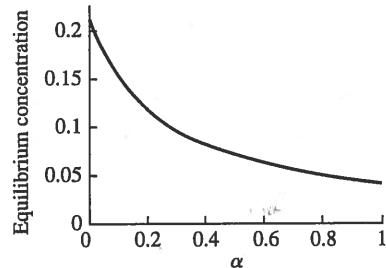


FIGURE 3.5.64

Equilibrium as a function of  $\alpha$

Rather surprisingly, the lung absorbs only about 10% of the available oxygen, leading to exhaled air that has nearly 30% less oxygen than ambient air. ▲

**Summary**

This section develops a mathematical model of chemical concentration in the lung. Starting from an understanding of how a lung exchanges air, we derived a discrete-time dynamical system for the chemical concentration. The discrete-time dynamical system can be described as a **weighted average** of the internal concentration and the **ambient concentration**. The equilibrium is equal to the ambient concentration, and cobwebbing diagrams indicate that solutions approach this equilibrium. Including absorption produces a slightly more complicated model, with an equilibrium that is less than the ambient concentration. We used this model to investigate the dynamics of oxygen in the lung.

**3.5****Exercises****Mathematical Techniques**

■ 1-2 ■ Use the idea of the weighted average to find the following.

1. 1 L of water at 30°C is mixed with 2 L of water at 100°C. What is the temperature of the resulting mixture?
2. In a class of 52 students, 20 scored 50 on a test, 18 scored 75, and the rest scored 100. What was the average score?

■ 3-6 ■ Express the following weighted averages in terms of the given variables.

3. 1 L of water at temperature  $T_1$  is mixed with 2 L of water at temperature  $T_2$ . What is the temperature of the resulting mixture? Set  $T_1 = 30$  and  $T_2 = 100$ , and compare with the result of Exercise 1.
4.  $V_1$  litres of water at 30°C is mixed with  $V_2$  litres of water at 100°C. What is the temperature of the resulting

mixture? Set  $V_1 = 1$  and  $V_2 = 2$ , and compare with the result of Exercise 1.

5.  $V_1$  litres of water at temperature  $T_1$  is mixed with  $V_2$  litres of water at temperature  $T_2$ . What is the temperature of the resulting mixture?

6.  $V_1$  litres of water at temperature  $T_1$  is mixed with  $V_2$  litres of water at temperature  $T_2$  and  $V_3$  litres of water at temperature  $T_3$ . What is the temperature of the resulting mixture?

■ 7-8 ■ The following are similar to examples of weighted averages with absorption.

7. 1 L of water at 30°C is to be mixed with 2 L of water at 100°C, as in Exercise 1. Before mixing, however, the temperature of each moves halfway to 0°C (so the 30°C water cools to 15°C). What is the temperature of the resulting mixture? Is this half the temperature of the result in Exercise 1?

8. In a class of 52 students, 20 scored 50 on a test, 18 scored 75, and the rest scored 100. The professor suspects cheating, however, and deducts 10 from each score. What is the average score after the deduction? Is it exactly 10 less than the average found in Exercise 2?

### Applications

► 9–12 ■ Suppose that the volume of the lung is  $V$  litres, the amount breathed in and out is  $W$  litres, and the ambient concentration is  $\gamma$  millimoles per litre. For each of the given sets of parameter values and the given initial condition, find the following:

- The amount of chemical in the lung before breathing.
- The amount of chemical breathed out.
- The amount of chemical in the lung after breathing out.
- The amount of chemical breathed in.
- The amount of chemical in the lung after breathing in.
- The concentration of chemical in the lung after breathing in.
- A comparison of this result with the result of using the general lung discrete-time dynamical system (Equation 3.5.1). Remember that  $q = W/V$ .

9.  $V = 2 \text{ L}$ ,  $W = 0.5 \text{ L}$ ,  $\gamma = 5 \text{ mmol/L}$ ,  $c_0 = 1 \text{ mmol/L}$

10.  $V = 1 \text{ L}$ ,  $W = 0.1 \text{ L}$ ,  $\gamma = 8 \text{ mmol/L}$ ,  $c_0 = 4 \text{ mmol/L}$

11.  $V = 1 \text{ L}$ ,  $W = 0.9 \text{ L}$ ,  $\gamma = 5 \text{ mmol/L}$ ,  $c_0 = 9 \text{ mmol/L}$

► 12.  $V = 10 \text{ L}$ ,  $W = 0.2 \text{ L}$ ,  $\gamma = 1 \text{ mmol/L}$ ,  $c_0 = 9 \text{ mmol/L}$

► 13–16 ■ Find and graph the updating function in the following cases. Cobweb for three steps, starting from the points indicated in the earlier problems. Sketch the solutions.

- The situation in Exercise 9.
- The situation in Exercise 10.
- The situation in Exercise 11.
- 16. The situation in Exercise 12.

► 17–20 ■ Find the lung discrete-time dynamical system with the following parameter values, and compute the equilibrium. Check that it matches the formula  $c^* = \gamma$ .

17.  $V = 2 \text{ L}$ ,  $W = 0.5 \text{ L}$ ,  $\gamma = 5 \text{ mmol/L}$ ,  $c_0 = 1 \text{ mmol/L}$

18.  $V = 1 \text{ L}$ ,  $W = 0.1 \text{ L}$ ,  $\gamma = 8 \text{ mmol/L}$ ,  $c_0 = 4 \text{ mmol/L}$

19.  $V = 1 \text{ L}$ ,  $W = 0.9 \text{ L}$ ,  $\gamma = 5 \text{ mmol/L}$ ,  $c_0 = 9 \text{ mmol/L}$

► 20.  $V = 10 \text{ L}$ ,  $W = 0.2 \text{ L}$ ,  $\gamma = 1 \text{ mmol/L}$ ,  $c_0 = 9 \text{ mmol/L}$

► 21–22 ■ The following problems investigate what happens if the breathing rate changes in the models of absorption examined in "Lung Dynamics with Absorption," Section 3.5. Use an external concentration of  $\gamma = 0.21$ , as before.

- Find the equilibrium oxygen concentration if the fraction of air exchanged is  $q = 0.4$  and the fraction absorbed is  $\alpha = 0.1$ . Can you explain why the concentration becomes higher even though the person is breathing more?

22. Find the equilibrium oxygen concentration if the fraction of air exchanged decreases to  $q = 0.1$  and the fraction absorbed decreases to  $\alpha = 0.05$ . Think of this as a person gasping for breath. Why is the concentration nearly the same as the value found in Example 3.5.9? Does this mean that gasping for breath is OK?

► 23–26 ■ The following problems investigate absorption that is not proportional to the concentration in the lung, as in "Lung Dynamics with Absorption," Section 3.5. Assume an external concentration of  $\gamma = 0.21$  and  $q = 0.2$ .

- Suppose that the oxygen concentration is reduced by 2% at each breath. Find the discrete-time dynamical system and the equilibrium. Are there values of  $c_t$  for which the system does not make sense?
- Suppose that the oxygen concentration is reduced by 3% at each breath. Find the discrete-time dynamical system and the equilibrium. Are there values of  $c_t$  for which the system does not make sense?
- Suppose that the amount absorbed is  $0.2(c_t - 0.05)$  if  $c_t \geq 0.05$ . This models a case where the only oxygen available is that in excess of the concentration in the blood, which corresponds roughly to 5%.

- 26. Consider a case like Exercise 25, but suppose that the amount absorbed is  $0.1(c_t - 0.05)$  if  $c_t \geq 0.05$ . Why is the concentration different from that found in Example 3.5.9?

► 27–28 ■ On the basis of the problems investigating absorption that is not proportional to the concentration in the lung (Exercises 23–26a), find the value of the parameter that produces an exhaled concentration of exactly 0.15. Assume  $\gamma = 0.21$  and  $q = 0.2$ .

- Suppose that the concentration is reduced by an amount  $A$  (generalizing the case in Exercises 23 and 24). Does the amount of oxygen absorbed match that found in Example 3.5.9?
- Suppose that the amount absorbed is  $\alpha(c_t - 0.05)$  (generalizing the case where only available oxygen is absorbed in Exercises 25 and 26a). Does the amount of oxygen absorbed match that found in Example 3.5.9?

► 29–30 ■ The following problems investigate production of carbon dioxide by the lung. Suppose that the concentration increases by an amount  $S$  before the air is exchanged. Assume an external concentration of carbon dioxide of  $\gamma = 0.0004$  and  $q = 0.2$ .

- Suppose  $S = 0.001$ . Write the discrete-time dynamical system and find its equilibrium. Compare the equilibrium with the external concentration.
- The actual concentration of carbon dioxide in exhaled air is about 0.04, or 100 times the external concentration. Find the value of  $S$  that gives this as the equilibrium.

► 31–32 ■ A bacterial population that has per capita production  $r < 1$  but is supplemented each generation follows a discrete-time dynamical system much like that of the lung. Use the following steps to build the discrete-time dynamical system in the two given cases.

- a. Starting from  $3 \cdot 10^6$  bacteria, find the number after reproduction.
- b. Find the number after the new bacteria are added.
- c. Find the discrete-time dynamical system.

**31.** A population of bacteria has per capita production  $r = 0.6$ , and  $1 \cdot 10^6$  bacteria are added each generation.

**32.** A population of bacteria has per capita production  $r = 0.2$ , and  $5 \cdot 10^6$  bacteria are added each generation.

**33–35** Find the equilibrium population of bacteria in the following cases with supplementation.

**33.** A population of bacteria has per capita production  $r = 0.6$ , and  $1 \cdot 10^6$  bacteria are added each generation (as in Exercise 31).

**34.** A population of bacteria has per capita production  $r = 0.2$ , and  $5 \cdot 10^6$  bacteria are added each generation (as in Exercise 32a).

**35.** A population of bacteria has per capita production  $r < 1$ , and  $1 \cdot 10^6$  bacteria are added each generation. What happens to the equilibrium if  $r = 0$ ? What happens if  $r$  is close to 1? Do these results make biological sense?

**36–39** Lakes receive water from streams each year and lose water to outflowing streams and evaporation. The following values are based on the Great Salt Lake in Utah. The lake receives  $3 \times 10^6 \text{ m}^3$  of water per year with salinity of 1 part per thousand (concentration 0.001). The lake contains  $3.3 \cdot 10^7 \text{ m}^3$  of water and starts with no salinity. Assume that the water that flows out is well mixed, having a concentration equal to that of the entire lake. Compute the discrete-time dynamical system by finding (a) the total salt before the inflow; (b) total water; (c) total salt and salt concentration after inflow; and (d) total water, total salt, and salt concentration after outflow or evaporation.

**36.** There is no evaporation, and  $3 \cdot 10^6 \text{ m}^3$  of water flows out each year.

**37.**  $1.5 \cdot 10^6 \text{ m}^3$  of water flows out each year, and  $1.5 \cdot 10^6 \text{ m}^3$  evaporates. No salt is lost through evaporation.

**38.** A total of  $3 \cdot 10^6 \text{ m}^3$  of water evaporates, and there is no outflow.

**39.** Assume instead that  $2 \cdot 10^6 \text{ m}^3$  of water evaporates and that there is no outflow. The volume of this lake is increasing.

**40–43** Find the equilibrium concentration of salt in a lake in the following cases. Describe the result in words by comparing the equilibrium salt level with the salt level of the water flowing in.

**40.** The situation described in Exercise 36.

**41.** The situation described in Exercise 37.

**42.** The situation described in Exercise 38.

**43.** The situation described in Exercise 39a.

**44–45** A lab is growing and harvesting a culture of valuable bacteria described by the discrete-time dynamical system

$$b_{t+1} = rb_t - h$$

The bacteria have per capita production  $r$ , and  $h$  are harvested each generation.

**44.** Suppose that  $r = 1.5$  and  $h = 1 \cdot 10^6$  bacteria. Sketch the updating function, and find the equilibrium both algebraically and graphically.

**45.** Without setting  $r$  and  $h$  to particular values, find the equilibrium algebraically. Does the equilibrium get larger when  $h$  gets larger? Does it get larger when  $r$  gets larger? If the answers seem odd (as they should), look at a cobweb diagram to try to figure out why.

### Computer Exercises

**46.** Use a computer to graph each trigonometric discrete-time dynamical system.

a.  $x_{t+1} = \cos x_t$

b.  $y_{t+1} = \sin y_t$

c.  $z_{t+1} = \sin z_t + \cos z_t$

Find the equilibria of each, and produce cobweb diagrams starting from three different initial conditions. Do the diagrams help make sense of the solutions?

**47.** Consider the discrete-time dynamical system

$$x_{t+1} = e^{ax_t}$$

for the following values of the parameter  $a$ . Use a computer to graph the function and the diagonal to look for equilibria. Cobweb starting from  $x_0 = 1$  in each case.

a.  $a = 0.3$

b.  $a = 0.4$

c.  $a = 1/e$

### Chapter Summary: Key Terms and Concepts

Define or explain the meaning of each term and concept.

**Discrete-time dynamical system:** updating function, initial condition; solution; basic exponential discrete-time dynamical system, basic additive discrete-time dynamical system, inverse (backward) dynamical system; equilibrium, stable and unstable equilibria; cobwebbing

**Applications:** per capita production, limited population model, model of selection; weighted average

## Concept Check: True/False Quiz

Determine whether each statement is true or false. Give a reason for your choice.

1. If  $m^*$  is an equilibrium of the system  $m_{t+1} = f(m_t)$ , then  $1/m^*$  is an equilibrium of the (backward in time) system  $m_t = f^{-1}(m_{t+1})$ .
2. The updating function of the system  $m_{t+1} = \frac{2m_t - 3}{m_t^2 + 1}$  is  $f(x) = x - \frac{2x - 3}{x^2 + 1}$ .
3. Assume that  $H_{t+1} = 2H_t + 3$ , where  $H_t$  and  $H_{t+1}$  are in metres. In units of millimetres, this dynamical system can be expressed as  $h_{t+1} = 2000h_t + 3000$ .
4. In the population model  $b_{t+1} = 4(b_t - 2b_t^2)$ , the per capita production rate is  $4(1 - 2b_t)$ .
5.  $m^* = 2$  is an equilibrium of the dynamical system  $m_{t+1} = e^{m_t - 2} + 1$ .
6. The system  $b_{t+1} = 3b_t + 120$  for the number of bacteria has no biologically significant equilibria.
7. The equilibrium  $m^* = 0$  of the dynamical system  $m_{t+1} = 1.02m_t$  is stable.
8. If  $m_{t+1} = 0.6m_t$  and  $m_0 = 0.2$ , then  $m_{t+1} = 0.2 \cdot 0.6^t$ .
9. The dynamical system  $b_{t+1} = b_t^3 - 2b_t^2 + 6$  has four equilibrium points.
10. 1 L of liquid with a concentration of 20 g/L of salt is mixed with 4 L of liquid with a concentration of 10 g/L. The resulting mixture has a concentration of 12 g/L.

## Supplementary Problems

1. A lab has a culture of a new kind of bacteria where each individual takes two hours to split into three bacteria. Suppose that these bacteria never die and that all offspring are OK.
  - a. Write an updating function describing this system.
  - b. Suppose there are  $2 \cdot 10^7$  bacteria at 9 A.M. How many will there be at 5 P.M.?
  - c. Write an equation for how many bacteria there are as a function of how long the culture has been running.
  - d. When will this population reach  $10^9$ ?
2. The number of bacteria in another lab follows the discrete-time dynamical system

$$b_{t+1} = \begin{cases} 2b_t & b_t \leq 1 \\ -0.5(b_t - 1) + 2 & b_t > 1 \end{cases}$$

where  $t$  is measured in hours and  $b_t$  in millions of bacteria.

- a. Graph the updating function. For what values of  $b_t$  does it make sense?
- b. Find the equilibrium.
- c. Cobweb starting from  $b_0 = 0.4$  million bacteria. What do you think happens to this population?
3. Find all equilibria for the population,  $p_t$ , whose per capita production is given by  $2p_t/(1 + p_t^2)$ .
4. Find the solution of the dynamical system

$$M_{t+1} = 0.5M_t + 1$$

with initial condition  $M_0 = 1$ . Hint: Assume that  $M_t = a(0.5^t) + b$  and use the technique that we introduced after Example 3.1.7 to find  $a$  and  $b$ . Verify that your solution is correct.

5. Consider the medication discrete-time dynamical system with both parameters from Examples 3.2.8 and 3.2.9:

$$M_{t+1} = (1 - \alpha)M_t + S$$

Find the equilibrium,  $M^*$ . Discuss possible ways of changing the parameters  $\alpha$  and  $S$  to make the equilibrium increase.

6. What is the concentration of a mixture of 2 mL of water with a salt concentration of 0.85 mol/L and 5 mL of water with a salt concentration of 0.7 mol/L?
7. As in Exercise 6, 2 mL of water with a salt concentration of 0.85 mol/L is to be mixed with 5 mL of water with a salt concentration of 0.7 mol/L. Before mixing, however, evaporation leads the concentration of each component to double. What is the concentration of the mixture? Is it exactly twice the concentration found in Exercise 6?
8. A population,  $b_t$ , of bacteria has per capita production  $r = 0.05b_t$ , and a fixed number  $B > 0$  of bacteria are added each generation. Discuss how the equilibrium of the population depends on  $B$ .
9. Identify the values (if they exist) of the parameter  $r$  for which the system

$$b_{t+1} = \frac{rb_t}{1 + 3b_t}$$

has no equilibria, for which it has one equilibrium, and for which there is more than one equilibrium.

10. Find all equilibrium points of the system

$$n_{t+1} = \frac{2n_t}{1 + 3n_t / 100}$$

11. The butterflies on a particular island are not doing very well. Each autumn, every butterfly produces on average 1.2 eggs and then dies. Half of these eggs survive the winter and

- produce new butterflies by late summer. At this time, 1000 butterflies arrive from the mainland to escape overcrowding.
- Write a discrete-time dynamical system for the population on this island.
  - Graph the updating function and cobweb starting from 1000.
  - Find the equilibrium number of butterflies.
12. Two similar objects are left to cool for one hour. One starts at  $80^{\circ}\text{C}$  and cools to  $70^{\circ}\text{C}$ , and the other starts at  $60^{\circ}\text{C}$  and cools to  $55^{\circ}\text{C}$ . Suppose the discrete-time dynamical system for cooling objects is linear.
- Find the discrete-time dynamical system. Find the temperature of the first object after two hours. Find the temperature after one hour of an object starting at  $20^{\circ}\text{C}$ .
  - Graph the updating function, and cobweb starting from  $80^{\circ}\text{C}$ .
  - Find the equilibrium. Explain what the equilibrium means.
13. A culture of bacteria increases in area by 10% each hour. Suppose the area is  $2 \text{ cm}^2$  at 2:00 P.M.
- What will the area be at 5:00 P.M.?
  - Write the relevant discrete-time dynamical system, and cobweb starting from 2.
  - What was the area at 1:00 P.M.?
  - If all bacteria are the same size and each adult produces two offspring each hour, what fraction of offspring must survive?
  - If the culture medium is only  $10 \text{ cm}^2$  in size, when will it be full?
14. Candidates Dewey and Howe are competing for fickle voters. Exactly 100,000 people are registered to vote in the election, and each will vote for one of these two candidates. Each week, some voters switch their allegiance. Twenty percent of Dewey's supporters switch to Howe each week. Howe's supporters are more likely to switch when Dewey is doing well: the fraction switching from Howe to Dewey is proportional to Dewey's percentage of the vote—none switch if Dewey commands 0% of the vote, and 50% switch if Dewey commands 100% of the vote. Suppose Howe starts with 90% of the vote.
- Find the number of votes Dewey and Howe have after a week.
  - Find Dewey's percentage after a week.
  - Find the discrete-time dynamical system describing Dewey's percentage.
  - Graph the updating function and find the equilibrium or equilibria.
  - Who will win the election?
15. An organism is breathing a chemical that modifies the depth of its breaths. In particular, suppose that the fraction,  $q$ , of air exchanged is given by
- $$q = \frac{c_t}{c_t + \gamma}$$
- where  $\gamma$  is the ambient concentration and  $c_t$  is the concentration in the lung. After a breath, a fraction  $q$  of the air came from outside, and a fraction  $1 - q$  remained from inside. Suppose  $\gamma = 0.5 \text{ mol/L}$ .
- Describe the breathing of this organism.
  - Find the discrete-time dynamical system for the concentration in the lung.
  - Find the equilibrium or equilibria.
16. Lint is building up in a dryer. With each use, the old amount of lint,  $x_t$ , is divided by  $1 + x_t$ , and 0.5 linton (the units of lint) is added.
- Find the discrete-time dynamical system and graph the updating function.
  - Cobweb starting from  $x_0 = 0$ . Graph the associated solution.
  - Find the equilibrium or equilibria.
17. Suppose people in a bank are waiting in two separate lines. Each minute several things happen: some people are served, some people join the lines, and some people switch lines. In particular, suppose that  $1/10$  of the people in the first line are served, and  $3/10$  of the people in the second line are served. Suppose that the number of people who join each line is equal to  $1/10$  of the total number of people in both lines and that  $1/10$  of the people in each line switch to the other.
- Suppose there are 100 people in each line at the beginning of a minute. Find how many people are in each line at the end of the minute.
  - Write a discrete-time dynamical system for the number of people in the first line and another discrete-time dynamical system for the number of people in the second.
  - Write a discrete-time dynamical system for the fraction of people in the first line.
18. A gambler faces off against a small casino. She begins with \$1000, and the casino starts with \$11,000. In each round, the gambler loses 10% of her current funds to the casino, and the casino loses 2% of its current funds to the gambler.
- Find the amount of money each has after one round.
  - Find a discrete-time dynamical system for the amount of money the gambler has and another for the amount of money the casino has.
  - Find the discrete-time dynamical system for the fraction,  $p$ , of money the gambler has.
  - Find the equilibrium fraction of the money held by the gambler.
  - Using the fact that the total amount of money is constant, find the equilibrium amount of money held by the gambler.

19. Let  $V$  represent the volume of a lung and  $c$  the concentration of some chemical inside. Suppose the internal surface area is proportional to the volume, and a lung with volume  $400 \text{ cm}^3$  has a surface area of  $100 \text{ cm}^2$ . The lung absorbs the chemical at a rate per unit surface area of

$$R = \alpha \left( \frac{c}{4 \times 10^{-2} + c} \right)$$

Time is measured in seconds, surface area in square centimetres, and volume in cubic centimetres. The parameter  $\alpha$  takes on the value 6 in the appropriate units.

- Find surface area as a function of volume. Make sure your dimensions make sense.
- What are the units of  $R$ ? What must the units of  $\alpha$  be?
- Suppose that  $c = 1 \cdot 10^{-2}$  and  $V = 400$ . Find the total amount of chemical absorbed.
- Suppose that  $c = 1 \cdot 10^{-2}$ . Find the total chemical absorbed as a function of  $V$ .

20. An Alberta millionaire (with \$1,000,001 in assets in 2014) got rich by clever investments. She managed to earn 10% interest per year for the last 20 years, and she plans to do the same in the future.
- How much did she have in 1994?
  - When will she have \$5,000,001?
  - Write the discrete-time dynamical system and graph the updating function.
  - Write and graph the solution.

21. A major university hires a famous Saskatchewan millionaire to manage its endowment. The millionaire decides to follow this plan each year:
- Spend 25% of all funds above \$10 million on university operations.
  - Invest the remainder at 10% interest.
  - Collect \$5 million in donations from wealthy alumni.
- Suppose the endowment has \$340 million to start. How much will it have after spending on university operations? After collecting interest on the remainder? After the donations roll in?
  - Find the discrete-time dynamical system.
  - Graph the updating function, and cobweb starting from \$340 million.

22. Another major university hires a famous Ontario millionaire to manage its endowment. This millionaire starts with \$340

million, brings back \$35.5 million the next year, and claims to be able to guarantee a linear increase in funds thereafter.

- How much money will this university have after eight years?
- Graph the endowment as a function of time.
- Write the discrete-time dynamical system, graph, and cobweb starting from \$340 million.
- Which university do you think will do better in the long run? Which millionaire would you hire?

23. Suppose traffic volume on a particular road has been as shown in the following table:

Year	Vehicles
1980	40,000
1990	60,000
2000	90,000
2010	135,000

- Sketch a graph of traffic over time.
- Find the discrete-time dynamical system that describes this traffic.
- What was the traffic volume in 1970?
- Give a formula for the predicted traffic in the year 2060.
- Find the half-life or the doubling time (whichever is appropriate) of the traffic volume.

24. In order to improve both the economy and the quality of life, policies are designed to encourage growth and decrease traffic flow. In particular, the number of cars is encouraged to increase by a factor of 1.6 over each 10-year period, but the commuters from 10,000 cars are to choose to ride comfortable new trains instead of driving.
- If there were 40,000 people commuting by car in 1980, how many would there be in 1990?
  - Find the discrete-time dynamical system describing the number of people commuting by car.
  - Find the equilibrium.
  - Graph the updating function, and cobweb starting from an initial number of 40,000.
  - In the long run, will there be more or less traffic with this policy than with the policy that led to the data in the previous problem? Why?

## Project

1. Combine the model of selection from the chapter with the models of mutation and reversion. Assume that wild type have per capita production  $r$ , mutants have per capita production  $s$ , a fraction  $\mu$  of the offspring of the wild type mutate into the

mutant type, and a fraction  $\nu$  of the offspring of the mutant type revert. First set  $b_i = 4 \cdot 10^6$ ,  $m_i = 2 \cdot 10^5$ ,  $\mu = 0.2$ ,  $\nu = 0.1$ ,  $r = 1.5$ , and  $s = 2$ .